

Article XX.—HONEY ANTS, WITH A REVISION OF THE  
AMERICAN MYRMECOCYSTI.

BY WILLIAM MORTON WHEELER.

INTRODUCTION.

For several years specimens of our American species of *Myrmecocystus* have been accumulating in my collection, and at various times I have devoted considerable attention to the habits of these remarkable ants in the arid lands of Texas, New Mexico, Arizona and Colorado. This material and these observations prove not only that the accounts of previous writers are very fragmentary but that the problems suggested by our *Myrmecocysti* are much more complicated than has been supposed. Since I may be unable to continue my field work on this group for some time to come, and since the preparation of a chapter on the honey ants for a forthcoming book has compelled me to examine the pertinent literature and the specimens in my collection with some care, I have decided to publish the following account of the material in hand.

Our *Myrmecocysti* present both taxonomic and ethological difficulties. We seem to have only two species, and these are closely related, but each is represented by several still more closely related geographical races, or subspecies and varieties. Although in part recognized by European myrmecologists, these subspecies and varieties have not been accurately defined. Such definition, indeed, could hardly be expected, for this is impossible without extensive studies in the field, because the workers of the same colony sometimes vary greatly in size and color and in some cases even tend to become dimorphic. Another difficulty, which seems not to have occurred to previous observers, arises from the fact that the extraordinary habit of producing honey-storing repletes, rotunds, nurses, or plerergates, as they have been designated by different writers, seems to be entirely absent in certain forms of both species, and that even in the forms in which it has been observed, this habit may, perhaps, be manifested only in particular localities or during certain seasons. These considerations tend to complicate the matter of classification, since the question must arise as to the taxonomic value of the presence or absence of this particular habit.

The ants of the genus *Myrmecocystus* are confined to the warmer and more arid portions of Europe, North Africa, Central Asia and Southwestern North America (Fig. 1). In these xerothermic regions they may be

said to take the place of the more moisture-loving species of *Formica*, to which they are very closely related. In fact, the two genera differ only in certain minor characters, such as the greater length in the worker and female *Myrmecocystus* of the fourth as compared with the fifth joint of the maxillary palpi and the more parallel frontal carinæ. In many, but not in all, species of the genus the wings of the male lack the discoidal cell, but this is present in the females. Comparison shows that there are certain striking differences between the Old World and North American species. The males of the American forms are small, resemble those of *Lasius* and have very simple genitalia. The workers and females have gular but no mental ammochætæ. In the Old World species the males are much larger and more like those of *Formica*, with more complicated genital valves, and the ammochætæ of the workers and females are developed as a tuft on the mentum and are absent on the gula. All of the Old World species are, moreover, highly carnivorous, whereas those of the New World have a varied diet: some being excessively carnivorous, while others, at least during certain seasons, are aphidicolous or feed on the sweet excretions of plants. Forel, many years ago (1886), called attention to some of these differences between the palearctic and neractic *Myrmecocysti*, and concluded that we ought, perhaps, to separate the latter, "retaining for them the name *Myrmecocystus* and reëstablishing the genus *Cataglyphis* Foerster for the other species." He hesitated to do this, however, because the female of *M. melliger* and *æneovirens*, and the worker and female of *Formica oculatissima* and *aberrans* were unknown and the winged sexes of *M. bombycinus* were imperfectly known. *M. æneovirens* has since been consigned to the genus *Melophorus*, and the winged sexes of certain forms of *M. melliger* have now been found. As they differ very little from those of *M. mexicanus* I believe that *Cataglyphis* should be reinstated, at least as a subspecific name.

Our North American *Myrmecocysti* are known to range over the arid plains and deserts of the southwest from the City of Mexico to Denver, Colorado. Of the two species, *M. melliger* is the more abundant at lower altitudes of about 300–1500 m., whereas *mexicanus* seems to find its optimum environment at about 2000–2500 m.

The earlier descriptions of these species are so meager that for a long time there was much misunderstanding in regard to their identity. Llave in 1832 first described a *Myrmecocystus* under the name of *Formica melligera* from specimens taken near the City of Mexico, but it is impossible to determine which of the species he had under observation, and there are no types in existence. In 1838 Wesmael described some ordinary workers and repletes of a Mexican ant as *Myrmecocystus mexicanus*. His types

have been preserved and one of these was examined by Emery (1893), who thus succeeded in establishing the identity of the species. Forel (1886) had previously seen specimens of a different *Myrmecocystus* taken in Texas (Collection de Saussure) and Mexico (Museum of Lyons) and had described it as *M. melliger*, believing that it was the species described by both Llave and Wesmael and that only one species existed. It is therefore necessary, as Emery has shown, to cite Forel and not Llave as the authority for *melliger*. Until the existence of two species had been established, the synonymy was in great confusion, and is still in that condition in Dalla Torre's 'Catalogus Hymenopterorum' (VII, 1893, pp. 217, 218). I give

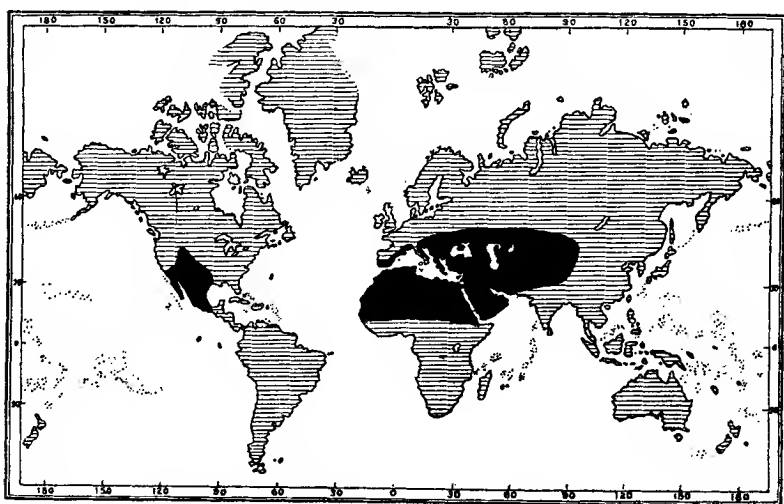


Fig. 1. Map showing (in black) the distribution of *Myrmecocystus sensu stricto* in North America and of the subgenus *Cataglyphis* in the Old World.

my interpretation of the references in connection with the following brief descriptions of the different forms, but many of the allusions of the earlier authors, especially those to Llave's *Formica melligera* must forever remain doubtful. Good specimens of the typical *melliger* and *mexicanus* seem to be rare in collections, and the males and females of these particular forms are still unknown. Nor have any full and accurate observations been published on their habits. For the present, therefore, we shall have to be content with the old accounts of Llave, Lucas and Wesmael, with McCook's much more satisfactory observations on a variety of *mexicanus*, and with my field notes on several of the forms of both species observed in the southwestern states.

## PART I. DESCRIPTIONS OF AMERICAN MYRMECOCYSTI.

1. *Myrmecocystus melliger* Forel.

(Fig. 2.)

*?Formica melligera* LLAVE, Reg. Trim. o Collect. Mem. Hist. Lit., 1832, p. 463, ♀.*Myrmecocystus melliger* FOREL, Ann. Soc. Entom. Belg., XXX, 1886, p. 202, ♀ (exclus. synonymy); EMERY, Zool. Jahrb., Abth. f. Syst., VII, 1893, pp. 666, 667; FOREL, Biol. Central. Amer., Hymenopt., III, 1899-1900, p. 130; DALLA TORRE, Catalog. Hymenopt., VII, 1893, p. 218 (in part).*Worker major*.—Length 8-9 mm.

Head rather large; excluding the mandibles, about as broad as long, a little narrower in front than behind, with rounded posterior corners and somewhat rounded or convex sides. Eyes small, less than  $\frac{1}{5}$  as long as the side of the head. Clypeus broad, convex in the middle, but not carinate, with broadly rounded but not projecting anterior border. Frontal area large, triangular, its outline indistinct behind. Frontal groove replaced by a rather indistinct ridge or raised line. Mandibles large, 7-toothed, with the apical tooth long and curved. Antennæ slender. Last joint of maxillary palpi but little more than  $\frac{1}{2}$  as long as the penultimate joint. Thorax long, constricted in the mesonotal region; in profile low and depressed above. Epinotum, when seen from above, broad, truncated behind; in profile with subequal base and declivity, meeting at a rounded and very obtuse angle. Petiole lower than the epinotum and about half as broad, thick, very blunt above, with a faint median impression. Gaster rather large, broadly elliptical, somewhat flattened above. Legs long.

Surface of body very finely punctate and shagreened; feebly shining, head more glabrous. Mandibles coarsely longitudinally striated.

Hairs and pubescence grayish, the former erect, rather abundant and covering all parts of the body, including the maxillary palpi, legs and antennal scapes. Pubescence dense on the gaster, petiole, thorax and legs, so that these parts have a silky luster, much shorter and sparser on the head, so that its shining surface is exposed.

Head and anterior portion of thorax yellowish red. Posterior portion of thorax, petiole, and legs more brownish red; gaster black but appearing gray on account of the layer of pubescence. Mandibular teeth and anterior border of clypeus blackish.

*Replete*.—Length 9-12 mm.

In all respects like the worker major except in having the gaster filled with honey and dilated to form a translucent sphere, as large as a pea (6-8 mm. in diameter), on the surface of which the sclerites appear as isolated dark patches separated by the tense, pellucid, yellowish intersegmental membrane.

*Worker minor*.—Length 4.5-5 mm.

Resembling the worker major, but with the head distinctly longer than broad, as broad in front as behind and with straight, subparallel sides. Color deeper, the red of the head, anterior portion of the thorax and legs being duller and more brownish.

Mexico: Guanajuato (Dugés), City of Mexico (Flohr), Matamoras (Langstroth), El Moral, Ciudad Porfirio Diaz (seven repletes from S. F. Rangel); Chilicote, Chihuahua (three ordinary workers from C. H. Tyler Townsend).

Texas: (Forel); Brownsville (Langstroth), El Paso (one worker, Am. Mus. Nat. Hist. Coll.).

The repletes from El Moral agree very closely with Forel's description. I am not so certain that the other specimens belong to the typical *melliger*. This form is distinguished from *mexicanus* by its small and more mesially

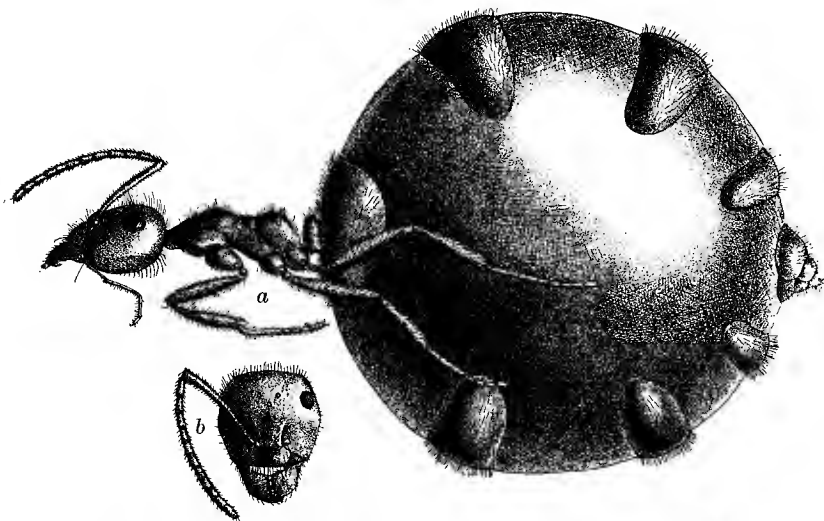


Fig. 2. *Myrmecocystus melliger* Forel, a, replete; b, head of same from above  $\times 8$ .

placed eyes, broader head in the worker major and darker color. Unfortunately both the female and male are unknown.

## 2. *Myrmecocystus melliger orbiceps* subsp. nov.

(Fig. 3.)

WHEELER, Biol. Bull., XIII, 4, 1907, p. 200, fig. 11, ♀.

*Worker major.* Length 7-8 mm.

Head fully as broad as long, orbicular, with much inflated and rounded cheeks. In other respects the structure of the body is like that of the typical form.

Surface finely and rather irregularly reticulate-punctate, opaque, except the head, which is shining. Mandibles coarsely longitudinally striated. Clypeus with a few scattered piligerous punctures.

Hairs and pubescence silver gray, the former erect, abundant, but rather short, slender and tapering; the latter long, very dense on the gaster, where it completely conceals the surface, somewhat shorter and less abundant on the thorax and legs and much less abundant on the head where the shining surface is exposed. The erect hairs on the antennal scapes and legs are usually abundant and very conspicuous though shorter than those on the body.

Rather vivid yellowish red, passing into brownish red on the epinotum, petiole, middle and hind coxæ and tips of the antennal funiculi. Gaster blackish but appearing silver gray and glossy on account of the dense pubescence.

*Worker minor.* Length 4-6.5 mm.

Head longer than broad, hardly broader behind than in front, with straight sub-parallel sides. Eyes relatively a little larger than those of the worker major, and antennæ more slender. Head less shining. Hairs and pubescence like those of the worker major, but somewhat shorter. Only the head yellowish red; the remainder of the body and the legs blackish; pronotum reddish in larger specimens.

*Female.* Length 11-12 mm.

Head rectangular; without the mandibles, as broad as long, with straight sub-parallel sides and straight posterior border. Eyes rather small, not more than  $\frac{1}{2}$  as long as the side of the head. Last joint of maxillary palpi not more than  $\frac{1}{2}$  as long as the penultimate joint. Thorax robust, through the wing insertions a little broader than the head, elliptical, nearly twice as long as broad, flattened above. Epinotum rounded, sloping, without distinct basal and declivous surfaces. Petiole compressed anteroposteriorly, with flat anterior and posterior surfaces and a blunt border, which is notched in the middle. Gaster broadly elliptical, somewhat flattened. Wings long (13-13.5 mm.), with large discoidal cell.

Sculpture, pilosity and pubescence similar to those of the worker major, but the thorax above is shining, like the head, and the hairs and pubescence are longer and more abundant on all parts of the body and especially on the head. The punctures on the head and mesonotum are coarser and the clypeus is covered with scattered foveolæ.

Blackish; with the pronotum and sides of the thorax suffused with red; head paler red but darker than in the worker. Legs and antennæ dark red. Gaster appearing silvery gray on account of the dense pubescence concealing the black ground color. Wings hyaline with yellow veins and stigma and the membranes suffused with yellow along the costal margin.

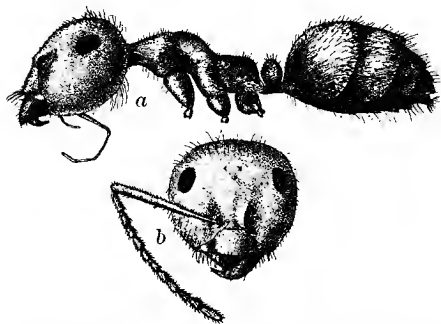


Fig. 3. *Myrmecocystus melliger orbiceps* subsp. nov., a, worker major in profile; b, head of same from above.  $\times 7$ .

Texas: Type locality: Bull Creek, near Austin (Brues, Melander, Wheeler); other localities: San Antonio, Marble Falls, San Angelo, Barksdale, Ft. Stockton, Langtry, Del Rio (Wheeler); Laredo (J. F. McClendon).

New Mexico: Alamogordo (H. L. Viereck, G. v. Krockow, A. G. Ruthven).

Arizona: Ash Fork and Tucson (Wheeler); Cochise County, 300-1500 m. (C. R. Biedemann).

This subspecies is certainly distinct from the typical *melliger* and is readily recognized by its more abundant and more silvery pubescence and pilosity, and the peculiar orbicular head of the worker major, which is sharply separated from the long-headed minor workers and may be compared with the singular soldier of the north African *M. bombycinus*, although the orb-headed form occurs in greater numbers in the colony.

### 3. *Myrmecocystus melliger mendax* subsp. nov.

(Fig. 4.)

*Worker major.* Length 6-7 mm.

Differing from the worker major of *orbiceps* as follows: Head smaller and rectangular, as broad as long, excluding the mandibles, with straight, subparallel sides, straight posterior border and rounded posterior angles. Cheeks not inflated. Color of the head a duller red and the infuscation of the thorax deeper, extending further forward and involving the pronotum. Silvery gray pubescence somewhat less abundant and erect hairs stouter and more obtuse, especially on the gaster.

*Worker minor.* Length 4-5.5 mm.

Like the corresponding form of *orbiceps*, except that the head is dark red behind, the hairs more obtuse and the pubescence somewhat sparser.

*Female.* Length 9-10 mm.

Resembling the female of *orbiceps* but with the thorax yellowish red, like the head, with the epinotum, pleuræ behind and below, and clouds on the parapsides and anteromedian portion of the mesonotum, fuscous. The legs, too, are paler than in *orbiceps*.

*Male.* Length 5-6 mm.

Head, including the eyes, as long as broad, narrowed in the region of the cheeks, which are longer than the eyes and somewhat concave. Mandibles larger, with two teeth, one apical, the other near the middle of the blade. Antennal scapes long and slender, first funicular joint enlarged distally, about three times as long as broad; remaining joints narrower, subequal and cylindrical. Thorax robust, broader than the head, shaped somewhat like that of the female. Petiole like that of the worker, but more acute above in profile. Genitalia resembling those of *Prenolepis*. Legs very slender, with large claws and pulvilli. Wings large, with well-developed discoidal cell.

Body shining, finely and irregularly punctate. Mandibles subopaque, not striated.

Hairs and pubescence similar to those of the worker, but the hairs more tapering and flexuous, and the pubescence more dilute, so that the surface of the body is more exposed.

Black; mandibles, antennæ, tarsi, and joints of legs piceous; bases of genital appendages whitish, tips brownish. Wings hyaline, the membranes somewhat sordid along the costal margin; veins and stigma pale fuscous or sordid yellow.

Colorado: Mt. Washington, near Colorado Springs, July 19 (types); Colorado City; Denver (Wheeler).

Arizona: Grand Cañon (Wheeler).

I should be inclined to regard this form as a mere variety of *orbiceps*

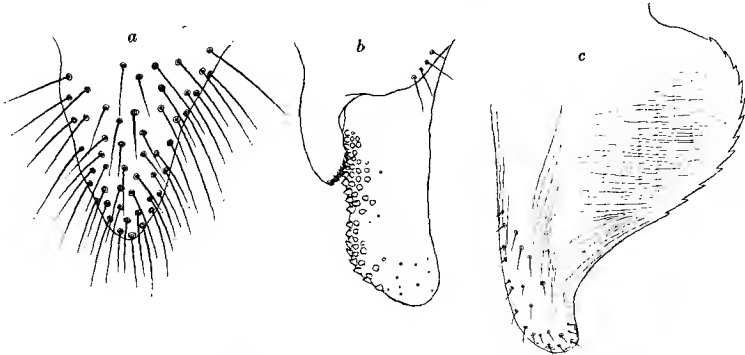


Fig. 4. *Myrmecocystus melliger mendax* subsp. nov., a, outer, b, median, c, inner genital valve of male.

were it not that the largest workers and the females are smaller and that no orb-faced individuals occurred in the three colonies which I excavated in Colorado. One of these colonies was very large and contained hundreds of workers and many males and females. The discoidal cell is constant in the wings of ten males in my collection.

#### 4. *Myrmecocystus melliger mendax* var. *comatus* var. nov. (Fig. 5.)

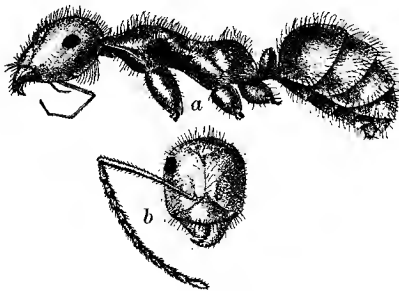


Fig. 5. *Myrmecocystus melliger mendax* var. *comatus* var. nov. a, worker major; b, head of same from above.  $\times 7$ .

This variety is closely related to the typical *mendax* but differs in having the erect hairs on the body decidedly longer, more abundant, tapering and flexuous. The coloration of all the phases is precisely like that of *mendax*. The male has a discoidal cell in the wing. Length of worker 3.5–6.5 mm.; female 10 mm.; male 6 mm. Described from numerous workers, one female and one male taken

from several large colonies at Ft. Davis, Texas, June 8 and 9, 1902.



### 5. *Myrmecocystus melliger mimicus* subsp. nov.

*Worker major.* Length 5-6 mm.

Resembling *mendax* but smaller and with different sculpture, color and pilosity. The gaster is shining, like the head, owing to the pubescence being much shorter and more dilute. Thorax and petiole subopaque. Erect hairs yellowish, similar to those of *mendax* but shorter, somewhat less abundant and on the legs more oblique. Head, thorax, petiole, antennæ and legs uniform deep brownish red; gaster black.

*Worker minor.* Length 3-4 mm.

Head proportionally longer and narrower than in the worker major. Thorax more or less infuscated, especially behind.

*Female.* Length 8-9 mm.

Sculpture and pilosity as in the worker. Head red, darker behind than in front. Thorax, petiole and gaster black or very dark reddish brown. Legs red, femora somewhat darker. Wings 10 mm. long, with yellowish veins and stigma; membranes very faintly suffused with yellow along the costal border.

*Male.* Length 4 mm.

Resembling the male *mendax* but decidedly smaller. Mandibles with only one tooth (the apical). Wings usually without a discoidal cell. The hairs are shorter and much less abundant and the surface of the body is more glabrous than in *mendax*. Wings faintly tinged with yellowish along their costal borders; veins and stigma very pale yellow. Mandibles, antennæ, legs and genitalia brown.

Texas: Chisos Mts. (W. B. Phillips); Alamito; Langtry; Ft. Stockton; Alpine; Del Rio; Monahans, Ward Co. (Wheeler).

New Mexico: Albuquerque, May 7, 1905 (Wheeler); Alamogordo (G. v. Krockow); Embudo and Deming (T. D. A. Cockerell); Las Truchas (Miss L. Gerhardt).

Arizona: Tucson; Phoenix; Jerome; Tempe; Yucca; Ash Fork (Wheeler).

California: Goshen Jc. (J. C. Bradley).

The types of this subspecies comprising numerous workers, six males and six females, are from Albuquerque. These males all lack the discoidal cell in the wings and the same is true of a single male from



Fig. 6. *Myrmecocystus mexicanus* var. *horti-deorum* McCook. Male, female, major and minor workers, slightly enlarged.

Langtry, Tex. Of six males taken from a single colony at Monahans, Tex., two have a complete discoidal cell, three have no trace of it and in one it is incomplete. The coloration of the workers is somewhat variable, but what I regard as the typical form of the subspecies has the head, thorax, petiole, legs and antennæ of a uniform deep red color and the gaster black and shining and without a silvery gray luster. Such individuals closely resemble certain forms of *Formica*, especially *F. fusca perpilosa* Wheeler and *F. nitidiventris* Emery.

6. *Myrmecocystus melliger mimicus* var. *jesuita* var. nov.



Fig. 7. *Myrmecocystus mexicanus* var. *horti-deorum* McCook. Repletes, slightly enlarged.

*Worker.* In size, sculpture and pilosity this form closely resembles the typical *mimicus*, but the thorax and posterior portion of the head are rather inconstant in coloration, varying from very dark red to black.

Ft. Davis, Texas (Wheeler).

The specimens of *mimicus* cited from Alamito and Alpine, Texas, are transitional to this variety as they have the thorax of a very deep red color.

7. *Myrmecocystus melliger mimicus* var. *depilis* Forel.

FOREL, Ann. Soc. Entom. Belg., XLV, 1901, p. 135 ♀; WHEELER, *ibid.*, p. 205.

*Worker minor.* Length 4–4.5 mm.

Shining and as dark in color as *jesuita*, but with much fewer erect hairs on the body and appendages. On the scapes the hairs are entirely or almost entirely lacking and are present only on the flexor surfaces of the tibiae.

Mexico: Pacheco, Zacatecas (Wheeler).

California: Needles, Mojave Desert (Wheeler).

A cotype of this variety from Pacheco, in my possession, has on the antennal scapes a few erect hairs but these are absent in the type described by Forel and in a single specimen from the Needles. The material, however, is insufficient, and the variety may have been based merely on rubbed specimens of what I have called *jesuita*.

### 8. *Myrmecocystus melliger semirufus* Emery.

*M. melliger* var. *semirufus* EMERY, Zool. Jahrb., Abth. f. Syst., VII, 1893, p. 667, ♀ ♂.

*Worker.* Length 3-4.5 mm.

Differing from the preceding forms of *melliger* in the smaller and more nearly uniform stature of the workers, and in color. Head, thorax, legs and antennæ light yellowish red, petiole brownish, gaster blackish or piceous. Surface of body rather shining. Hairs and pubescence somewhat sparser and shorter than in *mimicus*, gular ammochætæ longer than in any other form of *melliger*. Pubescence most abundant on the gaster to which it gives a grayish tinge and silky luster.

California: San Jacinto (Emery); Needles (Wheeler).

Arizona: Phoenix; Tucson; Yucca (Wheeler).

New Mexico: White Sands (G. v. Krockow).

Emery undoubtedly includes two distinct forms of *melliger* under the name *semirufus*: what I shall regard as the true *semirufus* from California and small workers of *mendax* from Denver, Colorado. He also describes male specimens but does not mention whether these came from California or Colorado. Judging from their size (5-6 mm.) they were probably from the latter state as we should expect both the male and female of *semirufus* to be even smaller than those of *mimicus*. A type specimen from California, received from Prof. Emery, is identical with all the specimens recorded from the above mentioned localities in that state, Arizona and New Mexico. I shall show in the sequel that *semirufus* is a very distinct form ethologically.

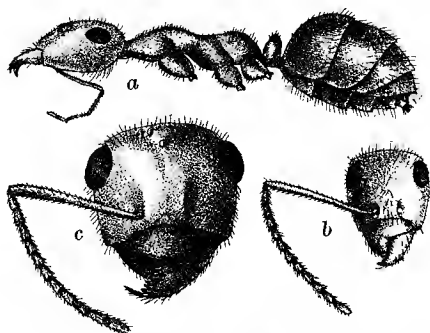


Fig. 8. *Myrmecocystus mexicanus* var. *hortideorum* McCook. a, worker, b, head of same, c, head of female.  $\times 10$ .

### 9. *Myrmecocystus melliger semirufus* var. *testaceus* Emery.

*M. melliger* var. *testaceus* EMERY, Zool. Jahrb., Abth. f. Syst., VII, 1893, p. 667, ♀.

*Worker.* Length 3-4.5 mm.

Entirely yellowish red. Sculpture, pilosity and pubescence much as in the typical *semirufus*. The pubescence is longest and densest on the gaster to which it gives a grayish color and silky luster.

California: San Jacinto (Emery); Claremont (C. F. Baker).

Emery attached this variety directly to *melliger* but that it is merely a color form of *semirufus* is shown by specimens taken from several colonies at Phoenix, Arizona and Needles, California. These specimens have the basal half of the gaster yellowish red and the apical half infuscated so that they are intermediate between *semirufus* and *testaceus*. Prof. Emery has kindly sent me a type specimen of the latter form.

# 10. *Myrmecocystus mexicanus* Wesmael.

? *Formica melligera* LLAVE, Reg. Trim. o Collect. Mem. Hist. Lit., 1832, p. 463; LUCAS, Rev. et Mag. Zool., 1860, pp. 269-280. ♀

? *Myrmecocystus melligerus* ROGER, Berl. Entom. Zeitschr., VI, 1862, p. 254.

? *Cataglyphis melligera* MAYR, Verh. zool. bot. Ges. Wien, XII, 1862, p. 701, no. 3.

*Myrmecocystus mexicanus* WESMAEL, Bull. Acad. Sc. Belg., V, 1838, pp. 756-761, ♀, figg. 1-4; WESTWOOD, Ann. Mag. Nat. Hist., VII, 1841, p. 145; F. SMITH, Cat. Hymen. Brit. Mus., VI, 1858, p. 200, ♀; Trans. Ent. Soc. London (3), I, 1862, Proc. p. 83; PAGENSTECHER, Jahrb. f. Litt. Heidelb., LIV, 1, 1861, pp. 172-176; FRIEPE Notiz., II, 1861, pp. 193-197; WEINLAND, Zool. Garten, II, 1861, p. 135; RILEY, Trans. Acad. Sci. St. Louis, III, Journ. of Proc. 1873, p. cix; EMERY, Zool. Jahrb., Abth. f. Syst., VII, 1893, p. 666; FOREL, Biol. Centr. Amer., Hymenopt., III, 1899-1900, p. 129; PERGANDE, Proc. Calif. Acad. Sci. (2), IV, 1893, p. 30.

*Worker.* Length 4.5-9 mm.

Differences between the major and minor workers much less marked than in *melliger*. Head, without the mandibles, distinctly longer than broad in the worker major and even longer in the smaller workers, narrower in front than behind, with rounded posterior corners; sides slightly convex in larger, straight in smaller individuals. Eyes large, more than  $\frac{1}{4}$  as long as the side of the head, placed further laterally and towards the posterior corners of the head than in *melliger*. Ocelli small. Clypeus very faintly carinate in front, its anterior border rounded and slightly projecting. Mandibles 9-toothed, their tips shorter and less curved than in *melliger*. Last joint of maxillary palpi a little shorter than the penultimate joint. Antennæ long and slender. Thorax long and narrow, constricted in the mesoepinotal region and in this region faintly concave in profile; pronotum low, faintly convex; epinotum more abruptly rounded, its base passing through a very rounded angle into the declivity; seen from above the epinotum is truncated behind, and as broad as long. Petiole less than half as broad as the epinotum, less thickened than in *melliger*, cuneate in profile, with flat anterior and posterior surfaces, with its blunt border faintly impressed in the middle. Gaster narrower, more convex above and more pointed behind than in *melliger*. Legs very long and slender.

Surface shining, very finely punctate-reticulate, but fainter than in *melliger*; mandibles finely and densely striatopunctate. Hairs and pubescence yellowish, shorter and less abundant than in the typical *melliger*, so that they do not conceal the shining surface. Erect hairs on legs and antennal scapes abundant, but little shorter than those on the body, rather obtuse. Pubescence more uniformly distributed and not much denser on the gaster than on the head.

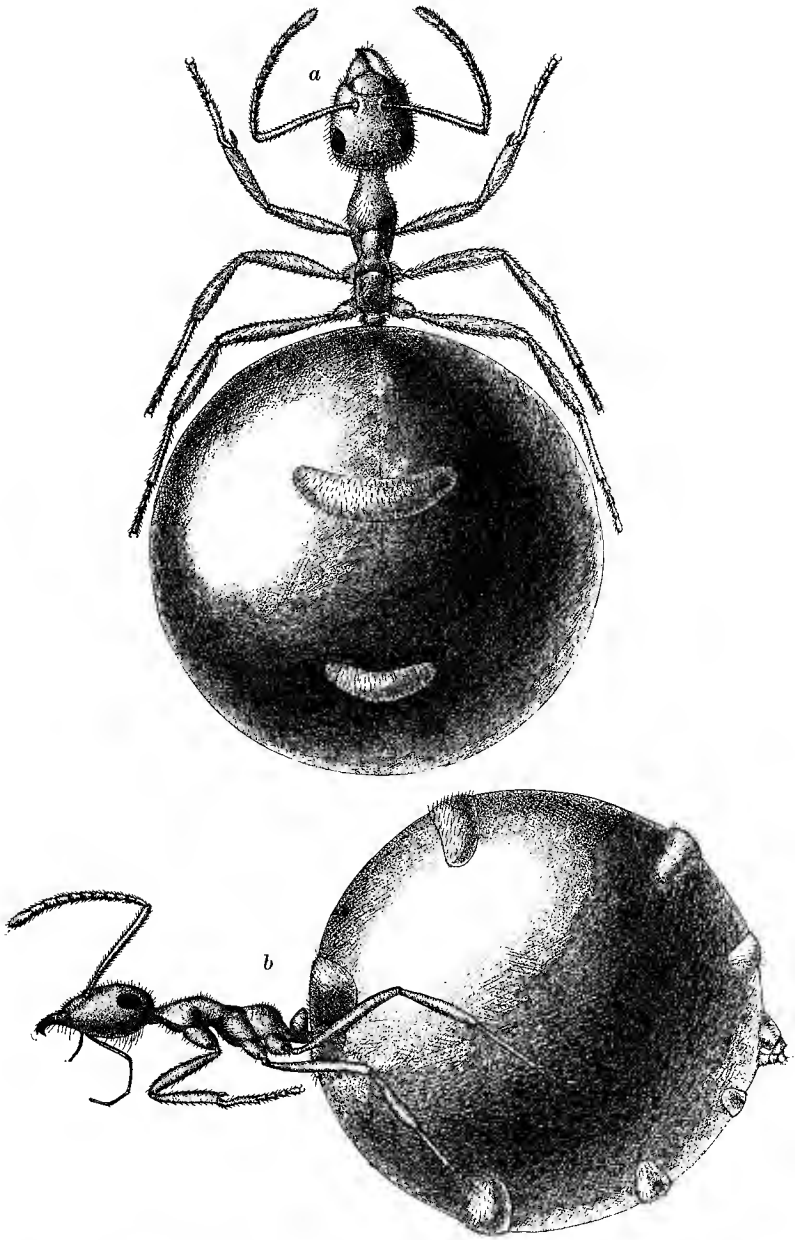


Fig. 9. *Myrmecocystus mexicanus* var. *horti-deorum* McCook. Replete, *a*, dorsal, *b*, lateral view.  $\times 10$ .

Testaceous or yellowish brown; posterior portion of head and upper portions of pro- and epinotum more or less infuscated; gaster fuscous. Teeth of mandibles blackish.

*Replete.* Length 10-13 mm.

Like the worker in all respects except that the gaster is distended to form a dull amber-colored sphere about the size of a pea.

Mexico: (Wesmael); San Luis Potosi, May 20, 1879 (E. Palmer); Santa Maria, Baja California (Eisen and Haines).

The description is drawn from a series of specimens from San Luis Potosi received from the Museum of Comparative Zoölogy. As these have been in alcohol nearly 30 years, their colors are not very well preserved, but the gaster is distinctly fuscous and the head and upper portions of the thorax are much darker than in the following variety and subspecies. I do not hesitate therefore to refer the specimens to the typical *mexicanus*.

# 11. *Myrmecocystus mexicanus* var. *horti-deorum* McCook.

(Figs. 6-10.)

- Myrmecocystus mexicanus* H. EDWARDS, Amer. Natur., VII, 1873, pp. 722-726; Proc. Calif. Acad. Sci. V, 1875, pp. 72-75; BLAKE, *ibid.*, p. 98; LOEW, Amer. Natur., VIII, 1874, pp. 365-366, ♀; SAUNDERS, Canad. Entom., VII, 1875, pp. 12-14, 1 fig.; MCCOOK, Proc. Phila. Acad. Nat. Sci. 1879, pp. 197-198; Ann. Mag. Nat. Hist. (5), IV, 1879, p. 474; Trans. Amer. Ent. Soc., VII, 1879, Proc. p. xxii.
- M. melliger* FOREL, Aertzt. Intelligenzbl. München, XXVII, 1880, p. 32; McCOOK, Amer. Entomol., III, 1880, pp. 273-274; Proc. Phila. Acad. Nat. Sci., 1881, pp. 170-230, pll. I-X; The Honey Ants of the Garden of the Gods, Phila., 1882, pp. 1-76, pll. I-X; ROMANES, Nature, XXV, 1882, pp. 405-406; KARSCH, Entomol. Nachr., VIII, 1882, pp. 186-191; HAGEN, Stettin. Entom. Zeitg., XLII, 1882, pp. 347-352; EMERY, Kosmos, XI, 1882, pp. 296-298; FOREL, Mitth. schweiz. Entom. Gesell., VII, 1, 1884, p. 4.
- M. melliger* var. *hortus-deorum* McCOOK, Proc. Phila. Acad. Nat. Sci., 1881, p. 75.
- M. hortus-deorum* FOREL, Ann. Soc. Ent. Belg., XXX, 1886, p. 202, ♀ ♂.
- M. horti-deorum* DALLE TORRE, Catalog. Hymen., VII, 1893, p. 217.
- M. mexicanus* var. *horti-deorum* EMERY, Zool. Jahrb., Abth. f. Syst., VII, 1893, p. 666.

*Worker.* Length 4.5-9 mm.

Differing from the typical Mexican form in color, which is yellow throughout, with the mandibles and posterior portion of the head slightly reddish. Mandibular teeth dark red. Basal surface of epinotum somewhat flatter than in *mexicanus*; the angle between the base and declivity less rounded and the anterior and posterior surfaces of the petiole somewhat more convex. Hairs and pubescence pale yellow or whitish, the former more slender and tapering.

*Replete.* Length 10-13 mm.

Like the larger workers except in having the gaster distended and filled with honey.

*Female.* Length 10–11 mm.

Head similar to that of the worker but as broad as long, without the mandibles. Apical tooth of mandibles very long and curved. Last joint of maxillary palpi little more than half as long as the penultimate joint, which like the third and fourth joints is broad and flat. Thorax like that of the *melliger* forms, broader than the head. Petiole in profile high, with flat anterior and posterior surfaces and rather acute border, notched in the middle. Gaster short, broadly elliptical, convex above. Legs moderately long. Wings long (12 mm.) with large discoidal cell.

Sculpture, pilosity and pubescence as in the worker. The yellow of the head, thorax and gaster is more brownish. Wings hyaline, with yellowish brown veins and stigma.

*Male.* Length 4.5–5.5 mm.

Very similar to the males of the *melliger* forms, but the mandibles have 2–3

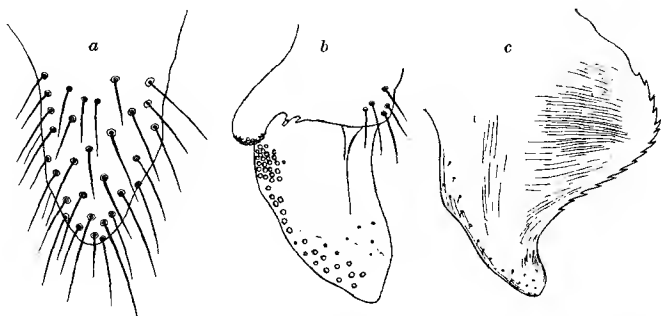


Fig. 10. *Myrmecocystus mexicanus* var. *horti-deorum*; a, outer, b, median, c, inner genital valve of male.

minute and unequal teeth in addition to the apical tooth. The discoidal cell is absent in the wing (I find it present and of abnormal triangular form in only one out of 25 specimens taken from several different colonies), and the genitalia have a different shape (Fig. 10).

Gaster shining, head and thorax more opaque, very finely punctate or shagreened.

Pilosity and pubescence similar to those of the worker but much less abundant, especially on the legs.

Pale yellow; head and gaster dark brown, thorax lighter brown, its sutures, the genitalia, mandibles, border of clypeus and antennæ whitish yellow; legs and the veins and stigma of the wings sordid yellow.

Colorado: Garden of the Gods, Manitou, Colorado City (McCook, P. J. Schmitt, Wheeler).

New Mexico: Santa Fe (Loew; Krummeck; R. Thaxter, Wheeler Exped.); Abiquiu (Cope); Pecos (T. D. A. Cockerell).

California (McCook).

Redescribed from a number of workers and females from all of these localities except California, and from topotypes of males and females taken July 25–28, 1903 and 1906. This variety is very constant and might be regarded as a subspecies, but before elevating it to this rank, it would be desirable to have more material of the typical form from several localities in Mexico.

12. *Myrmecocystus mexicanus navajo* subsp. nov.

(Fig. 11.)

*Worker.* Length 3–4.5 mm.

Differing from the two preceding forms

in its much smaller size and in the following characters: the whole body is of a pale whitish yellow color, except the gaster which is more or less fuscous owing to the dark contents of the crop showing through the diaphanous yellow integument. The eyes are decidedly larger, being more than  $\frac{1}{3}$  as long as the side of the head. The declivity of the epinotum is longer than the base and slightly concave, the petiole is narrow, anteroposteriorly compressed, and its free border is rounded and entire. The hairs and pubescence are much sparser than in the other forms of the species. The scapes have erect hairs only on their anterior surfaces and the legs only on the flexor surfaces of the femora. In some speci-

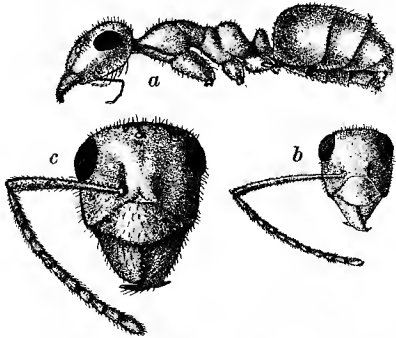


Fig. 11. *Myrmecocystus mexicanus navajo* subsp. nov., a, worker; b, head of same; c, head of female.  $\times 10$ .

mens there are also a few oblique hairs on the flexor surfaces of the tibiae. The surface of the body is uniformly shining and the pubescence is very dilute.

*Female* (deâlated). Length 9 mm.

Head narrower than in *horti-deorum*, with slightly larger eyes. Yellow color of body paler, pilosity and pubescence sparser.

This form, which is very distinct both in structure and habits is described from a large number of workers and a single female taken May 7 and 25, 1905, from several colonies in the dry deserts east of the town of Albuquerque, New Mexico.

13. *Myrmecocystus mexicanus mojave* subsp. nov.

*Worker.* Length 4.5–5 mm.

Resembling the worker of *navajo* in stature, in the shape of the head and size of



the eyes, but differing from this and the other forms of *mexicanus* in having the neck much shorter, so that the pronotum, seen from above, is as broad as long. Hairs and pubescence white, more abundant than in *horti-deorum* and *mexicanus*. Color pale sordid yellow, with the posterior portion of the head brown and the legs and antennæ whitish.

California: Ontario (J. C. Bradley).

Described from two dozen specimens, some of which are in a partially replete condition, with the ingluvies full of honey dew.

## PART II. ETHOLOGICAL NOTES AND DESCRIPTIONS.

### 1. The Typical Mexican Forms of *Myrmecocystus*.

The early accounts of the habits of *Myrmecocystus* in the papers of Llave, Wesmael and Lucas are based on hearsay, as none of these authors saw living specimens. That these accounts refer, perhaps, to two different species is of no great moment, since they are couched in very general terms.

In addition to some notes on a few alcoholic specimens, Llave gives the following description of the habits of his *Formica melligera*: "A careful observer, who lives in the town of Dolores, in the vicinity of which the formicaries are found, told me that, out of curiosity, he had excavated some of the nests belonging to the ants which the peasants call *busileras*. He assured me that the inhabitants of these nests are a species of small ant which does not make an earthen mound at the entrance of its dwelling, and that in following the excavations and removing the earth, one comes upon a kind of gallery from the ceiling of which the *busileras* hang suspended and huddled together, covering both the roof and the walls of the gallery. He told me also that the peasant women and children are well acquainted with these nests, that they seek them assiduously for the purpose of obtaining the honey and that when they are going to make a present of them, they take hold of them very cautiously, carefully remove the head and thorax and then place them in a dish; but if the insects are to be eaten as soon as found, the saccharine portion is sucked out and the remainder thrown away. The head and thorax are removed, I was told, to prevent the ants from injuring one another, for although they are unable to walk, owing to the prodigious volume of the abdomen, they nevertheless struggle when placed in a dish, and catch hold of and rupture one another, so that in the end they become flaccid and depleted. Indeed, the skin which unites the segments of the abdomen is so delicate and especially so distended, on account of the enormous quantity of honey which it contains, that the least puncture causes the

contents to flow out. They say that when this operation, namely the removal of the head and thorax, is not performed, the honey diminishes and, according to the peasants, is consumed by the ants.”<sup>1</sup>

Concerning the function of the replete worker Wesmael promulgated an erroneous conception which he gleaned from the statements of Baron de Normann, who brought the types of *M. mexicanus* to Belgium. He says: “According to the statement of M. de Normann, this species of ant constructs subterranean habitations, which the individuals with vesiculate abdomens never leave. There, condemned to almost complete immobility, their unique function is to elaborate a kind of honey, which is then disgorged into special reservoirs analogous to the waxen cells of bees. Unfortunately M. de Normann saw only a fragment of this kind of comb, too distorted to give an accurate idea of its structure, and he could not bring it to Europe, as he knew not how to preserve it during the voyage. For my part, I am much inclined to believe in the reality of the facts reported by our honorable envoy; first, because I have no reason to doubt his veracity; and second, because these facts follow almost of necessity from the structure of these singular ants; for how can we impute the active habits of their congeners to individuals all of whose movements must be impeded by the volume and weight of their abdomen, which, moreover, would have its delicate walls torn by contact with the slightest projection? On the other hand, since these ants, in their capacity as workers, have the ovaries completely suppressed, the volume of the abdomen can be attributed only to an excessive development of the digestive organs it contains, a development which must originate in the superabundance of nourishment brought to these sedentary ants by the other workers; and these workers in turn, would not waste their time and efforts in furnishing their big-bellied companions with such a copious amount of food, if the latter did not return it to the community with interest. Hence the big-bellied ants are only the cooks, so to speak, who prepare food and provisions without other utensils than their stomach.

“One is much inclined to ask, whether in the colonies of the Mexican ants, the big-bellied individuals are already such on quitting the pupal stage. In the absence of positive information on this point, we may suppose that the excessive development of the abdomen is, perhaps, merely the result of over-feeding, coupled with perpetual inactivity. It is well known that in our own species certain individuals who have reached an age when the sexual organs lose their activity, sometimes take on, in the midst of repose and abundance, an enormous abdominal amplitude. It is also

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<sup>1</sup> I have here translated Lucas's translation of Llave, as I have been unable to find the original even in the beautiful library of the new Hispanic Museum.

known that the same causes produce the same effects in the domestic animals, which we fatten after they have been castrated. Be this as it may, however, it is worth remarking, that in the ants under consideration, the vesiculate abdomen contains no organs; or rather, it is itself only a huge sac-shaped stomach, beginning at the second segment and terminating in the anus."

In May, 1852, Langstroth presented to the Philadelphia Academy some repletes of a *Myrmecocystus* which his brother had collected at Matamoras, Mexico. The low altitude of the locality shows that they belonged to *M.*

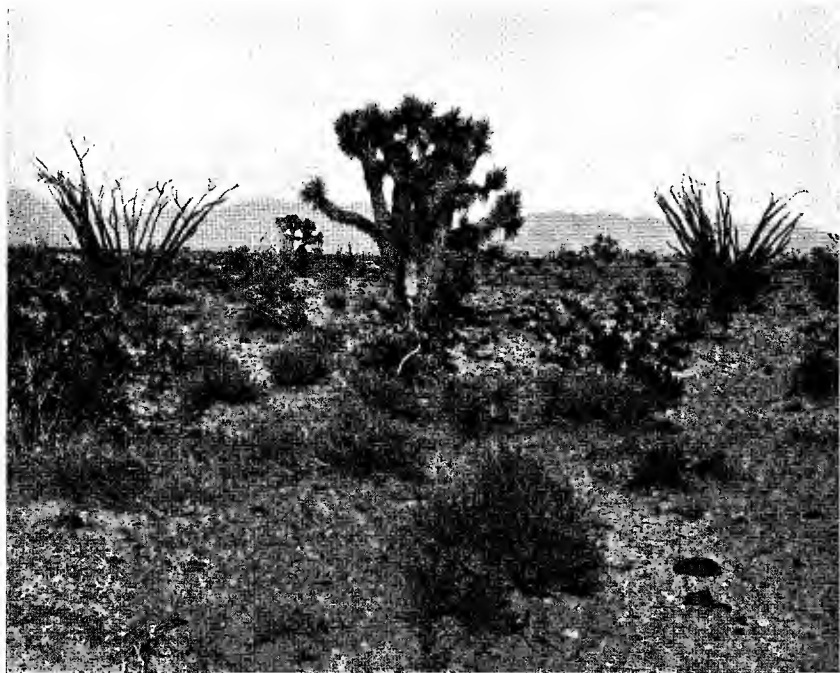


Fig. 12. Desert at Yucca, Arizona; home of *Myrmecocystus melliger mimicus* subsp. nov.

*melliger*. These repletes were correctly described "as living repositories for the surplus honey of the colony, which in time of need answer the purpose of the full honey-combs of the bee." At the same meeting Leidy reported on the gastric anatomy of the specimens, asserting that the honey is contained within the greatly distended stomach and that "all the other viscera of the abdomen are completely obliterated, and even the tracheal vessels have entirely disappeared, which is an important physiological fact, as by the supply of oxygen being cut off, none of the honey is consumed in the

process of respiration." In June of the same year Wetherell (1852) presented to the Academy the results of a chemical analysis of the honey of the Langstroth repletes. He found that the average weight of the honey in one of these individuals was 0.3942 gr., the average weight of the ant 0.048 gr., so that "the honey which an average one of these ants contains is 8.2 times greater than the weight of its body. . . . The syrup extracted from the ant had an agreeable sweet taste, the odor very much resembling that of the syrup of squills. It reacted slightly acid to blue litmus paper. When evaporated by the heat of steam, it dried to a gummy mass, which did not exhibit traces of crystallization after standing for a couple of weeks. It was very hygroscopic, becoming quickly soft from the absorption of water from the atmosphere." As a result of further analysis Wetherill found that "the honey contained in the Mexican ant is a nearly pure solution of the sugar, so-called, of fruits, which is in a state of hydration, isomeric with grape sugar,  $C_{12}H_{14}O_{14}$  and differing from grape sugar in not crystallizing." The source of the acidity he could not determine, but raised the question as to whether it was formic acid or acetic from the oxidation of the alcohol in which the specimens had been preserved.

These remarks and the meager descriptions of the original specimens of *M. mexicanus* and perhaps also of *melliger*, comprise all the observations that seem to have been published on the typical Mexican forms of the genus. The following observations relate exclusively to the forms occurring in the United States.

## 2. *Myrmecocystus melliger orbiceps* subsp. nov.

This beautiful form differs from all our other *Myrmecocysti* in the glittering white sheen of its body. In this respect it is not unlike the Saharan *M. bombycinus*, which, when running rapidly over the desert soil, is said to resemble a rolling drop of quicksilver. *M. orbiceps*, too, prefers very hot, dry localities. I have found it along the limestone escarpment which stretches from Austin to Del Rio and forms the Edwards Plateau of Texas, and in the deserts of Trans Pecos Texas, New Mexico and Arizona. It may be most conveniently studied on the Jollyville Plateau, a few miles west of Austin, and at San Pedro Springs on the outskirts of San Antonio. Like the Saharan *Myrmecocysti* it runs over the ground with great agility in the full glare of the sun.

The nest, which is always in stony soil, has the form of an obscure crater, with an irregular or arcuate and sometimes very large entrance (2-3.5 cm. in diameter) leading down obliquely into the soil. The main gallery thus formed breaks up at a depth of 20-30 cm. into short passages and flat,

irregular chambers. The colonies are rather small, comprising hardly more than 300-500 individuals, and therefore resemble colonies of certain species of *Formica* (*subpolita*, *munda*, *schaufussi*). Among the workers one always finds a few, sometimes less than a dozen, of the large, orb-headed individuals (Fig. 3) which characterize this subspecies. All the workers contain an abundance of formic acid, with which they seem to defend themselves in much the same manner as the species of *Formica*. A few of them, confined in a vial, are soon suffocated with their own secretions. Winged females were taken April 21 and 27.

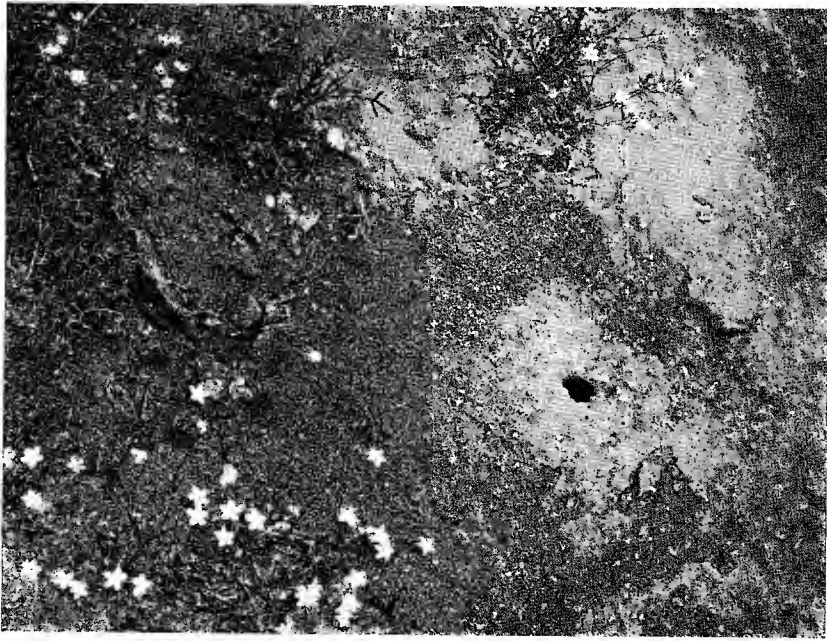


Fig. 13. Nest crater of *Myrmecocystus melliger mimicus* subsp. nov. in adobe soil. Tucson, Arizona. About  $\frac{1}{4}$  natural size.

On first examining the colonies of *orbiceps* on the lime-stone hills near Austin, I was greatly impressed with the complete absence of anything resembling the repletes of the typical *melliger*. Again and again, at various seasons of the year and in different localities, I excavated nests, but was never able to observe the slightest tendency to gastric distension in any individuals of the colony. The ants were never seen climbing about on the low desert vegetation in search of aphid excrement or the sweet secretions of galls or flowers. It was not difficult, however, to ascertain the character

of their food. On one occasion, while watching a nest, I saw many of the workers returning with male and female termites that had been captured just after their nuptial flight. Others were bringing in dead harvesting ants (*Pogonomyrmex*). In some of the nests whole chambers were set aside as kitchen middens and were filled with the remains of a great variety of insects. I am convinced, therefore, that *M. orbiceps* is a highly predaceous and carnivorous ant like the various palearctic *Myrmecocysti* described by Forel (1890 a and b, 1895), Lameere (1902) and Escherich (1902).

### 3. *Myrmecocystus melliger mendax* subsp. nov.

This subspecies closely resembles the preceding both in its appearance and in its nesting habits, but has a more northerly distribution. I have seen it only in Colorado. During the summer of 1903 I found a single colony near Colorado City, a second much more flourishing colony near Mount Washington, south of Colorado Springs, and in 1906 a third was found nesting between the cracks of a stone sidewalk in Denver. This is the northernmost point to which any of our *Myrmecocysti* have been traced.

I came upon the Mount Washington colony July 18 at 4.10 P. M. soon after a shower and just as the sun emerged from a bank of clouds. The males and females were issuing for their marriage flight from a nest which was in coarse pebbly soil around the roots of a cactus. I should not have found the colony had not my attention been attracted by the throng of feverish workers surrounding the entrance whence the sexual forms were issuing. There was nothing unusual about the flight: the males and females climbed about on the pebbles and plants with quivering wings and antennæ and rose into the air one by one. As it was late in the afternoon, the nest was marked for excavation on the following day and I walked towards the town. I had gone less than a quarter of a mile when I found several females that had already descended from their flight, removed their wings and were running over the ground in search of a place in which to establish their formicaries. On the following day the nest was excavated with great care in the hope that it might contain repletes, but I was disappointed. Remains of insects in some of the chambers showed that this subspecies, like *orbiceps*, is carnivorous. The nest still contained several males and deâlated females which had either returned voluntarily after the marriage flight on the previous day or had not participated in it.

The var. *comatus*, which is merely a more hairy form of *mendax*, was observed only in Hospital Cañon at Fort Davis, Texas. Some of the nests were near oak trees (*Quercus cinerea*), which the ants were ascending, apparently for the purpose of visiting aphids on the foliage, but none of the

returning individuals had their gasters enlarged and I was unable to find repletes in any of the nests. Some of the nests, however, had large kitchen middens of insect fragments near their entrances, showing that this ant is predatory like *orbiceps* and the typical *mexicanus*. The absence of repletes in this instance did not surprise me because some nine months of rainless weather had preceded my visit to Fort Davis, a period more than sufficient to exhaust any store of honey that might have been collected during the previous year.

4. ***Myrmecocystus melliger mimicus* subsp. nov.**

This is the most abundant and widely distributed form of the genus from Trans Pecos Texas to the Mojave Desert and probably throughout Chihuahua and Sonora. It prefers the pebbly or pure adobe soil of the more arid deserts (Fig. 12). Here it constructs rather regular craters 10–15



Fig. 14. Nest crater of *Myrmecocystus melliger semirufus* Emery. Needles, California. About  $\frac{1}{4}$  natural size.

cm. across at the base and 3–4 cm. high, with a circular opening varying from 1.5–2 cm. in diameter (Fig. 13). I have carefully excavated a great number of colonies of *mimicus* and its var. *jesuita*, in widely separated localities but have never been able to observe in the workers the slightest

tendency to develop repletes. The ants live in such arid and barren places that it is difficult to understand how they can obtain sufficient moisture for their daily needs, to say nothing of storing it up for future consumption. The workers are diurnal like those of the preceding subspecies and varieties and prey upon insects.

5. *Myrmecocystus melliger semirufus* Emery.

This is a very distinct form characterized by the small size and feeble polymorphism of its workers, and occurs only in the pure sand of the river-bottoms and gullies in the deserts. It is not uncommon along the Gila River near Phoenix, Arizona and the Colorado River near Needles, California. Its craters (Figs. 14 and 15) are somewhat larger and more regular



Fig. 15. Nest crater of *Myrmecocystus melliger semirufus* Emery, under all-thorn (*Koeberlinia*) bush, Mojave Desert, California. About  $\frac{1}{2}$  natural size.

than those constructed by *Lasius americanus* in warm, sandy places in the Eastern States. At Needles the workers were found attending peculiar coccids (*Orthezia*) which were feeding on some small desert shrubs. This would point to the existence of repletes in the nest, but although I excavated a number of these, a task that was greatly facilitated by the loose consistency



of the sand, I found nothing but workers of the ordinary size and form. At the time I was under the impression that I had succeeded in excavating many of the nests very thoroughly, but as I never unearthed a queen, and as ant-nests in sand are apt to extend far below the surface, I admit that *semirufus* may develop repletes in chambers to which I failed to get access. Nothing is known concerning the habits of the var. *testaceus*, but it, too, probably lives in pure sand.

#### 6. *Myrmecocystus mexicanus* var. *horti-deorum* McCook.

The earliest account of this insect was communicated by Capt. W. B. Fleson of Santa Fe, New Mexico to Henry Edwards (1873). This account, which may be more properly called a fanciful improvisation, impressed Edwards as being so valuable that he communicated it to Charles Darwin and published it both in the 'Proceedings of the California Academy of Sciences' and the 'American Naturalist.' McCook, who a few years later, as we shall see, made a careful study of *horti-deorum*, was inclined to reject the story, but Romanes (1883) republished the whole article, together with the absurd diagram accompanying it, in his book on 'Animal Intelligence,' as a sterling contribution to the study of ant psychology! One may reject lucubrations like those of Capt. Fleson, Lincecum, Buckley and other exuberant observers of ants, with a few vehement comments, pass them by without remark, or accord them a certain amount of interpretative study. On the whole, I find the last to be the preferable course.

According to Edwards the colonies observed by Capt. Fleson at Santa Fe "consist of three distinct kinds of ants, probably of two separate genera, whose offices in the general order of the nest would seem to be entirely apart from each other, and who perform the labor allotted to them without the least encroachment upon the duties of their fellows. The larger number of individuals consists of yellow worker ants of two kinds, one of which of a pale golden yellow color, about one third of an inch in length, acts as nurses and feeders of the honey-making kind, who do not quit the interior of the nest, 'their sole purpose being, apparently, to elaborate a kind of honey, which they are said to discharge in the prepared receptacles, and which constitutes the food of the entire population. In these honey-secreting workers the abdomen is distended into a large, globose, bladder-like form, about the size of a pea.'" The third variety of ant is much larger, black in color, and with very formidable mandibles. For the purpose of better understanding the doings of this strange community, we will designate them as follows:

No. 1.— Yellow workers; nurses and feeders.

No. 2.— Yellow workers; honey makers.

No. 3.— Black workers; guards and purveyors.”

Then follows a description of the nest and the behavior of the guards which perform certain ridiculous military tactics on three sides of a square. One section of the black warriors is described as “entering the quadrangle by a diagonal line bearing N E, and carrying in their mouths flowers and fragments of aromatic leaves which they deposit in the center of the square.”



Fig. 16. Garden of the Gods, near Manitou, Colorado, looking north; showing the rocky ridges on which *Myrmecocystus horti-deorum* nests.

The interior of the nest, which has two entrances, is depicted as follows: “By removing the soil to a depth of about three feet, and tracing the course of the galleries from the entrances (b) and (d), a small excavation is reached, across which is spread in the form of a spider’s web, a net work of squares spun by the insects, the squares being about one-quarter inch across, and the ends of the web fastened firmly to the earth of the sides of the hollowed space which forms the bottom of the excavation. In each of the squares, supported by the web, sits one of the honey-making workers (No. 2),

apparently in the condition of a prisoner, as it does not appear that these creatures ever quit the nest. Indeed it would be difficult for them to do so, as their abdomens are so swollen out by the honey which they contain, as to render locomotion a task of difficulty, if not to make it utterly impossible. The workers, (No. 1), provide them with a constant supply of flowers and pollen which, by a process analogous to that of the bee, they convert into honey."

In 1875 Saunders published a few observations made on *horti-deorum* in the mountains around Santa Fe by Krummeck who says that he has "sat



Fig. 17. Shin-oaks (*Quercus undulata*) in the Garden of the Gods.

by their nests and watched them working, for, at one time, six or seven hours; the workers carry leaves of different plants home, to feed, as I suppose, the others that produce the honey." Saunders adds that "Mr. Krummeck has tried to procure us specimens of the plants on which this insect feeds, but has not yet succeeded. He does not think that the honey is deposited by these honey ants in cells, as has been stated, but that they keep the fluid in their bodies, and the workers feed from them, and that when the honey in the sac of an individual is exhausted, it dies. In reference to the uses made of this honey in New Mexico, he says that the natives make a very pleasant drink of it, which is made in the proportion of three

or four drachms of the honey to six ounces of water. It has not commercial value, is not brought to market, but simply made for their own use. They use this drink among themselves in the mountains in cases of fever, where medical attendance cannot be obtained. The honey is also used by them as a cure for eye diseases, especially for cataract." The following is one of the most interesting remarks in Saunders's paper: "In early life none of these insects present any unusual distension of the body, but when arrived at a certain period of maturity some individuals begin to show a distended



Fig. 18. Nest crater of *Myrmecocystus horti-deorum*, from above; Red Rock Cañon, near Manitou, Colorado. About  $\frac{1}{4}$  natural size.

abdomen, which after a time becomes swollen into a comparatively immense sphere, produced by the distension of the membrane connecting the abdominal segments, this sphere or sac being filled with a sort of honey. Another class of individuals in the community, raised from the same brood of eggs, manifest no tendency of this sort, but retain the usual normal form of the abdomen." At first sight this looks like a *bonâ fide* observation, but the context shows that it is merely a restatement in somewhat clearer and more positive form of Wesmael's supposition above quoted (p. 362). It occurs, in fact, in a paragraph reviewing the work of the Belgian author. There

is therefore nothing to indicate that Krummeck made any observations of his own on the development of the repletes of *M. horti-deorum*.

We see how Baron de Normann's supposition that the repletes produce honey continued to influence the thoughts of succeeding writers. Capt. Fleeson improvised the gossamer receptacles and both he and Krummeck were of the opinion that the ants used their stomachs as a kind of distillery for making honey out of flowers and leaves. In commenting on Fleeson's vagaries McCook says: "One can hardly refrain from the thought that



Fig. 19. Nest crater of *Myrmecocystus horti-deorum* built at edge of stone. Red Rock Cañon, Colorado. About  $\frac{1}{4}$  natural size.

Capt. Fleeson was testing the credulity of the writer by one of those jokes of which naturalists are occasionally the victims. But, if the narrative is to be taken in good faith, I can only explain the facts by supposing, first, that the observer happened upon a nest of cutting ants (*Atta ferveus*), within whose boundaries a nest of *Melliger* had chanced to be established, and had confounded the habits of the two as those of one formicary; or, second, that the cutting-ant, or some other species of similar economy, has really acquired the habit of kidnapping and domesticating the honey ant for the

sake of its treasured sweets, precisely as many ants domesticate aphids, or, as the slave-making ants, *Formica sanguinea* and *Polyergus lucidus*, domesticate *Formica fusca* and *F. schaufussi*." I am inclined to believe with McCook, that both Fleeson and Krummeck confounded two totally different species of ants — *M. horti-deorum* and some leaf-cutter, or Attiine ant. The carrying of the flowers and leaves must refer to the latter and the web mentioned by Fleeson would seem to be an attempt to describe the fungus garden of some Attiine ant. But if these suppositions are correct, we must assume that both authors either jumbled together observations which they had made in very different parts of New Mexico, or merely reported from hearsay, for quite apart from the fact that there is no known leaf-cutting ant that agrees with Fleeson's worker No. 3, it may be rather positively stated that there are no leaf-cutting ants in the neighborhood of Santa Fe, which has an elevation of more than 2000 m. We surely cannot suppose that the *Atta fervens* (= *texana*) to which McCook refers, occurs there, because this ant is peculiar to the low-lying and rather humid portions of Texas. I am therefore of the opinion that neither Fleeson's nor Krummeck's accounts contain anything of value except the mere record of the occurrence of *M. horti-deorum* at Santa Fe. Equally worthless is a brief description by Blake (1873) of the gastric structure in some specimens of this ant presented to the California Academy by Edwards, since he confidently asserts that the intestine of the replete "is not continued beyond the thorax," and seems to imagine that the honey is contained in the body cavity!

In 1874 Loew, who was chemist and mineralogist to the Lieutenant Wheeler Exploring Expedition, published a few notes on *M. horti-deorum*, which he, too, observed at Santa Fe. He describes the nest correctly in the main, and then remarks that "the opinion that the honey is discharged into receptacles is entirely erroneous; the only receptacle is their own abdomen swollen up to the size of a pea, clear, transparent," etc. The honey of the repletes is described as "slightly acid in summer from a trace of formic acid, but perfectly neutral in autumn and winter; it contains a little more water than the honey of bees, and has therefore somewhat greater limpidity." Like previous writers he seems to believe that the ants produce the honey in addition to storing it, and makes the utterly impractical suggestion that "it would be worth while for beekeepers to try to introduce them into some kind of bee-hive with a suitable dry soil and the proper food at hand for them."

We owe to McCook (1882) the first and, up to the present time, the only trustworthy and adequate account of the habits of any of the American *Myrmecocysti*. His work is so well known and accessible that I may confine myself to a brief outline of its contents. He discovered *horti-deorum*

in the Garden of the Gods near Manitou, Colo. (Fig. 16). The nests, which were found on the tops of stony ridges, are described in great detail. The large circular entrance 2-2.5 cm. in diameter is in the center of a cone-shaped crater of pebbles 8-25 cm. in diameter at the base and 5-8 cm. high (Figs. 18 to 20). The entrance opens into a vertical or oblique gallery which at a depth of 9-15 cm. breaks up into several smaller galleries. These usually extend to one side of the entrance gallery. At a depth of 20-35 cm. the smaller galleries lead into chambers with smooth, flattened floors and



Fig. 20. *Myrmecocystus horti-deorum* nest, with two craters. Red Rock Cañon, Colorado. About  $\frac{1}{2}$  natural size.

rough, vaulted ceilings. These chambers vary from 12-15 cm. in length and 7-10 cm. in width, and may be 4 cm. high in the middle. McCook has described some very large fornicaries, the galleries of one of which covered an area of more than 2 sq. m. and reached a depth in the soil of more than a meter. In the chambers the repletes hang, side by side, by means of their claws from the vaulting which is evidently left rough as an adaptation to this peculiar habit (Fig. 21). These individuals are capable of more movement than has usually been supposed, but if they fall from the ceiling they are unable to regain their pendent position without assistance.

McCook effectively dispels the notion that the repletes manufacture the honey, by showing how they obtain and store it. *M. horti-deorum* is decidedly nocturnal, unlike the different subspecies and varieties of *melliger*, which are diurnal. Indeed, the etiolated appearance and pale yellow color of the northern forms of *mexicanus* at once suggest a fondness for darkness, just as the deeper tints of the typical form of the species suggest diurnal or crepuscular habits. During the day, therefore, the workers of *M. horti-deorum* are never seen outside of the nest, but frequently a guard of workers

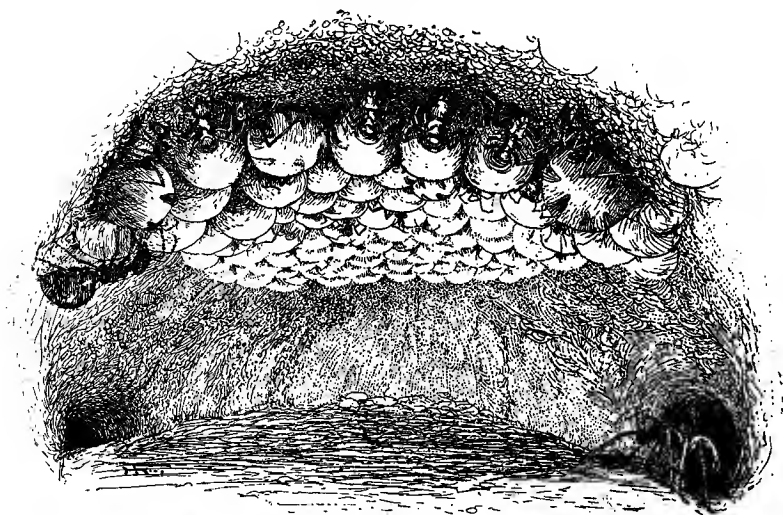


Fig. 21. Repletes of *Myrmecocystus horti-deorum* hanging from roof of honey chamber. (After McCook.)

is stationed just within the large opening, apparently for the purpose of preventing other ants, spiders, etc. from entering the nest. McCook found that during July the workers leave the nest in a file at about 7.30 P. M. and visit the shin oaks (*Quercus undulata*) which grow abundantly along the rocky ridges in the Garden of the Gods and the surrounding country (Fig. 17.) The twigs of these oaks are often covered with small woody galls about the size of a pea and of a more or less conical or spheroidal shape, the work of the Cynipid *Holcaspis perniciosus* Bassett.<sup>1</sup> At night these

<sup>1</sup> Riley in 1880 briefly described these galls under the name of *Cynips quercus-mellaria*, but he did not breed the insect that produces them. This was described by Bassett in 1890 as *Holcaspis perniciosus* and was taken from galls collected in Utah. I have not seen Bassett's types, but a lot of galls labelled "*H. perniciosus*, Garden of the Gods" in the Bassett collection of the American Museum of Natural History are unquestionably the same as those described and figured by McCook in 1882 as Riley's *C. quercus-mellaria*. I should be inclined to accept this as the specific name of the insect, for there can be no doubt concerning the identity of the galls, were it not that there seems to be a growing unwillingness on the part of cecidologists to recognize names based merely on the plant deformations.



galls exude minute droplets of a sweet, watery secretion (Fig. 23). This is eagerly collected by the ordinary workers, carried to the nest in their crops and fed to the repletes, which thus function as living bottles or casks, storing the precious liquid so that it can be drawn upon when other sources of food are exhausted.

Forel, in 1880, disproved Leidy's and Blake's statements by showing that the gaster of the replete *horti-deorum* owes its size and rotundity exclusively to an enormous distension of the crop, or ingluvies and not of the

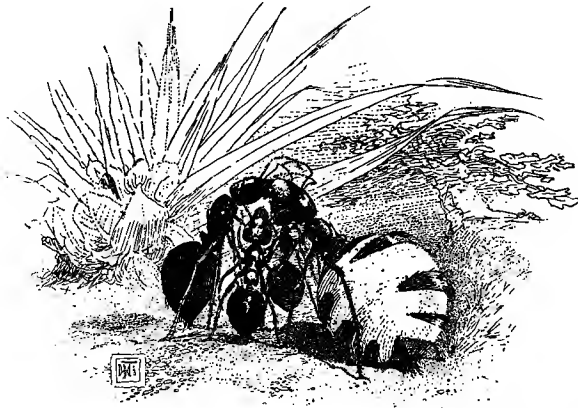


Fig. 22. Replete *Myrmecocystus hortideorum* in the act of regurgitating food to workers of the ordinary form. (After McCook.)

stomach, and that all the other structures found in the gaster of the ordinary worker are present in the replete, though they are necessarily crowded up against the gastric wall. These observations were confirmed by McCook's careful dissections and figures of the gaster of ordinary workers, semi-repletes ("semirotunds") and repletes. He inferred that "the process by which the rotundity of the honey-bearers has probably been produced, has its exact counterpart in the ordinary distension of the crop in overfed ants; that, at least, the condition of the alimentary canal, in all the castes, is the same, differing only in degree, and therefore, the probability is very great that *the honey-bearer is simply a worker with an overgrown abdomen.*" He found, moreover, that "a comparison of the worker with the honey-bearer shows that there is absolutely no difference between them except in the distended condition of the abdomen" and he therefore inferred "that the worker majors, for the most part, and sometimes the minors, are transformed by the gradual distension of the crop, and expansion of the abdomen, into the honey-bearers, and that the latter do not compose a distinct caste.

It is probable, however, that some of the majors have a special tendency to this change by reason of some peculiar structure or form of the intestine and abdominal walls." Although McCook gave these excellent reasons for believing that the replete must develop from a worker of the ordinary type, he did not actually witness the transformation. His account covers a great many other details in the behavior of *M. horti-deorum*, but as many of these are common to most other Camponotine ants, I need not discuss them in this connection.

My own observations on *M. horti-deorum* were made during July and August 1903 and 1906. At first I worked in the Garden of the Gods and located several nests on the ridges where McCook made his observations many years ago. But the region is now so overrun by tourists that careful and continuous observation of ant-nests is out of the question. I therefore sought new localities and was soon able to find a number of fine nests south of the Fontaine-qui-Bouille, along Bear Creek and Red Rock Cañons. A few nests were also found at a much greater distance from the Garden of the Gods, west of Manitou and south of the Ute Pass. In all of these localities there are thickets of shin oaks (*Quercus undulata* and *gambeli*) and the nests are situated only on the summits of dry, stony ridges, just as they are in the Garden of the Gods.

During the two summers I excavated fully a dozen fine colonies of *horti-deorum* and was able to confirm in nearly every detail McCook's interesting account of the nest architecture and the habits of the ordinary and replete workers. I was unable to make observations at night but have no doubt that McCook's account of the foraging habits is perfectly accurate and trustworthy. I am inclined to believe, however, that the exudations of the *Holcaspis* galls may furnish only a portion of the food of the ants and that these insects may obtain much, if not most of their honey from the coccids and aphids on the oaks and other plants in the neighborhood. It would be strange,

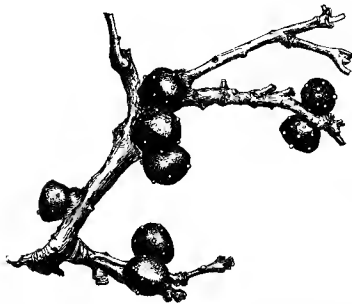


Fig. 23. Galls of *Holcaspis perniciosus* on twigs of *Quercus undulata*, showing the exuding droplets which are collected by the workers of *Myrmecocystus horti-deorum*. About  $\frac{2}{3}$  natural size.

indeed, if these ants did not take advantage of this food supply which undoubtedly must be greater than that obtainable from the galls.

I have been able to prove what has been surmised by previous observers, namely, that workers of the ordinary size and form develop into repletes. In the nests which I excavated during July there were many workers,

males and females. While keeping several colonies in artificial nests it occurred to me that the change from the ordinary to the replete worker must begin during the callow stage while the integument of the gaster is still very soft and distensible. I accordingly isolated a number of young callows in two of my nests and fed them with maple syrup and cane sugar water. They partook of the substances greedily, and a few of the workers in each nest gradually began to assume the replete condition. During the course of four to six weeks several of them became what I call semirepletes (McCook's "semirotunds") and four of them, three in one nest and one in the other, actually attained the dimensions of the perfect replete. Most of the workers, however, showed no inclination to assume this form. In most cases, as McCook has shown, it is the major workers that most readily tend to become repletes, but this is not an invariable rule. In the honey chambers of opulent colonies I have usually found a few replete mediæ and minimæ hanging among the larger but no more turgid sisters. Thoroughly hardened workers of the ordinary form, according to my observations, are no longer able to become repletes. It is probable, therefore, that McCook's failure to secure repletes from isolated major workers was due to his using individuals that were too old.

Why certain callows should aspire to become animated pots or casks, while others prefer to be active foragers and providers, is an enigma. I do not believe, however, that this is due to differences in the "structure or form of the intestine and abdominal walls," as McCook suggests. It is more probably an unusual example of the division of labor, which is shown by careful study to exist in various forms and degrees among all ants with monomorphic workers. The individual worker performs different duties at different stages in its life, beginning in its callow stage as a mere nurse, then becoming a forager, warrior or guard and in its old age sometimes encroaching on the function of the queen by becoming a parthenogenetic mother. It is not improbable that many worker ants acquire habits—using this word, for the moment, in its restricted and technical sense as employed in human psychology—and tend to perform throughout life the special function which they happened to assume while in the callow stage. This may account for the development of the replete both in the individual and the species not only in *M. horti-deorum* but in all other honey ants.

While excavating the nests above mentioned, I was impressed with certain peculiarities in their structure and situation, which seem to be explainable only as adaptations to the development of repletes. One of these peculiarities is the great hardness of the soil that is preferred by the ants. This is the more astonishing because the workers are such slender and delicate organisms. It is evident that hard soil is best suited to the construction

of vaulted chambers like those in which the repletes hang, whereas soft or friable soil would be most disadvantageous. The development of repletes also makes it necessary for the ants to seek very dry situations for their nests. Hence we always find them, in the environs of Manitou at least, on the summits of ridges which shed the rain very rapidly. The honey chambers must be kept very dry both to prevent the disastrous results of crumbling and slipping walls and to obviate the growth of moulds on the repletes, which are, of course, imprisoned for life in dark cavities and filled



Fig. 24. Desert near Albuquerque, New Mexico; home of *Myrmecocystus mexicanus navajo* subsp. nov.

with substances that readily favor the development of fungi. I believe also that the size of the nest openings and galleries, which are so much larger than would seem to be required by such small, slender ants, may be an adaptation to securing plenty of fresh air in the honey chambers. If these suppositions are correct there is obviously a reciprocal relation between the replete habit and an arid environment: the ants store honey because they are living in an arid region where moisture and food are precious and the storing of honey in replete workers, in turn, is possible only in very dry soil.

7. *Myrmecocystus mexicanus navajo* subsp. nov.

This subspecies bears somewhat the same relation to *M. horti-deorum* that *semirufus* does to *melliger*, that is, it is a small, pale, depauperate form. I found its nests to be rather common, though widely scattered, in the desert south of Albuquerque, New Mexico (Fig. 24). A few were seen even in the streets of the town. They are, however, so very inconspicuous that my

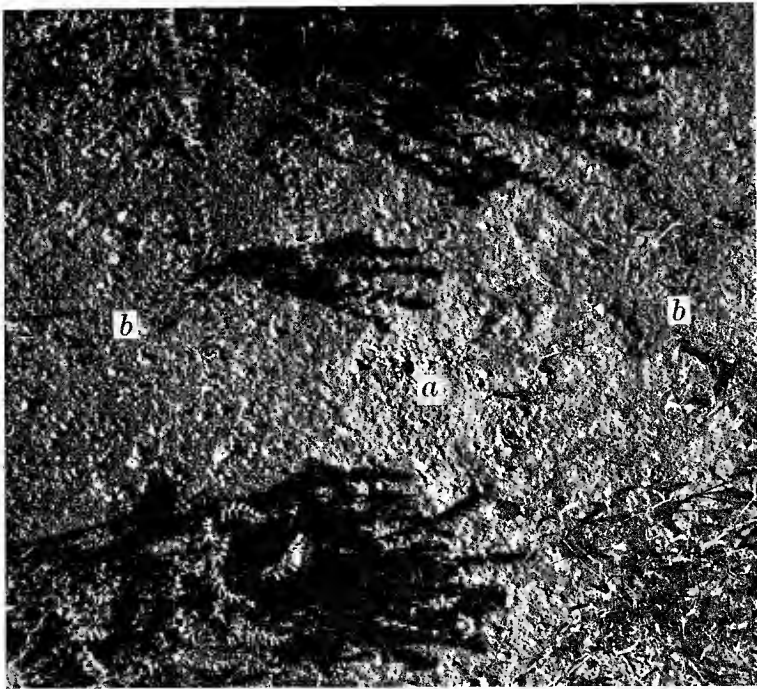


Fig. 25. Nest of *Myrmecocystus mexicanus navajo* subsp. nov. near Albuquerque, New Mexico. Entrance in middle of figure, at *a*; vestiges of crater shown as fine granulations at *b*. About  $\frac{1}{3}$  natural size.

finding them was the merest accident. The entrance (Fig. 25*a*) is very small, not more than .5–1 cm. in diameter and is not surrounded by a conical crater as in nearly all the other American *Myrmecocysti*. A vestige of this structure may nevertheless be said to be present, for a very thin layer of small pellets of earth is scattered by the ants over a circular area, 30–60 cm. in diameter, around the entrance (Fig. 25*b*). Immediately encircling the entrance, however, there is a zone free from pellets.

I excavated twenty-two of these nests and found their internal structure

to be like that of the *horti-deorum* nests, except that the galleries are more tenuous and the chambers smaller and less distinct. The latter lie at a depth of 20–25 cm. The colonies, too, are much smaller than those of *horti-deorum* and comprise hardly more than 100–150 workers. No traces of repletes could be found in any of the nests although several of these were so completely excavated that I obtained the mother queen. All the nests contained larvæ and cocoons but no males were taken on the two occasions when I collected at Albuquerque (May 7 and 28).

There can be no doubt that *M. navajo* is a distinctly nocturnal ant. It is even paler and more etiolated than *horti-deorum*. I was unable to learn anything about its feeding habits. The dry mesa on which it lives has an elevation of about 1300 m. and at the time of my second visit was covered with blooming desert plants (*Yucca*, *Ephedra*, *Astragalus*, *Dalea*, *Fallugia*, etc.). These, in all probability, support aphids, coccids and membracids which in turn furnish *M. navajo* with food, for I can hardly believe that this delicate little ant is carnivorous.

### PART III. HONEY ANTS OF VARIOUS GENERA AND THE SIGNIFICATION OF THE REPLETE.

The foregoing account shows that both of the North American species of *Myrmecocystus* are sufficiently plastic to have produced several races and that these differ from one another more in their habits than in their structure. In the same species, *melliger*, as we have seen, there are forms that produce repletes and seem to feed almost exclusively on sweet juices, and other that are highly carnivorous and are not known to have workers with distended crops. We must conclude, therefore, either that the observations represent the permanent condition of the colonies, in other words, that certain races always and others never develop repletes, or that repletion, which is merely a physiological state, is an inconstant character. The latter conclusion implies that only certain colonies, at certain times in their development, or when nesting in certain regions, where the sweet exudations of aphids and plants abound, develop repletes, whereas colonies of the same races nesting in a different environment have become increasingly predatory and carnivorous. After studying these ants and excavating many of their nests at all seasons of the year and in many localities in the southwest I am inclined to believe that the replete habit is confined to certain subspecies and varieties, both in *M. melliger* and *mexicanus*, but am compelled to admit that some or all of these forms may be sufficiently plastic to assume either the replete or the predatory habit according to circumstances. This doubt

has prevented me from describing the predatory forms of *M. melliger* as distinct species. I leave the matter to be decided by some future investigator who can devote months or even years to the study of our desert ants.

Although my observations are incomplete, they prove nevertheless that the conditions in the majority of the subspecies and varieties cannot be the same as those described for *M. horti-deorum*. If such deserticolous forms as *M. orbiceps*, *mendax*, *mimicus*, *semirufus* and *navajo* ever produce repletes, the sweet liquid used for this purpose cannot be obtained from oak-galls, for the very simple reason that oaks do not grow in the deserts. And as the low, dry, halophytic and xerophytic vegetation of these regions develops very few galls of any kind, honey would have to be supplied by coccids and aphids, and these, too, are by no means abundant on desert plants.

That repletion, nevertheless, may be merely a sporadic or temporary condition among the different American *Myrmecocysti* seems to be indicated by the manner of its occurrence among other ants. It will therefore be advisable to review the observations that have been made on the replete habit in general, especially as such a review will also show some of the phylogenetic stages through which the typical *M. melliger* and *mexicanus* and the variety *horti-deorum* have, in all probability, passed.

Repletes are known to occur only in the Camponotinae and Dolichoderinae, the two subfamilies comprising the ants most given to feeding on the sweet excretions of Homoptera and the exudations of the galls and nectaries of plants. Structurally these ants differ from most of the species of Ponerinae, Dorylinae and Myrmicinae in having a thinner and more pliable chitinous investment over the whole body, and especially over the gaster. When out foraging on the surfaces of plants the individual worker is therefore able to collect and carry home a considerable amount of honey by greatly distending its crop. This leads to a separation of the gastric sclerites and the transparent intersegmental membrane is exposed to view, permitting the light to shine through the limpid contents of the crop, while the remaining abdominal organs are crowded up against the posterior wall. This distension, which may be called incipient repletion, is often seen in the workers of our various species of *Formica*, *Lasius*, *Camponotus*, *Prenolepis*, *Brachymyrmex*, etc. that are returning to the nest from a visit to their herds of aphids and coccids. Any of the workers of the colony, especially while in their callow or semicallow stages, may assume this incipient repletion, which is very slight compared with the perfect repletion of *Myrmecocystus*.

The relatively insignificant distension of the gaster in the foraging workers of the ants above mentioned is the generalized basis from which the more specialized condition of the true honey ants has arisen, first, by restricting the repletion to certain workers in the colony (physiological division of

labor), and second, by exaggerating the distensibility of the ingluvial and gastric walls in these individuals. Certain callows, engaged in feeding the young, had a tendency to remain in the nest and receive the honey brought in by foragers. At first they were simple receivers, able to move about freely through the chambers and galleries of the nest, and distribute the food to the larvæ and their fellow ants, but in the course of time, by increasing their capacity, they became receptacles, without power of locomotion and suspended themselves from the ceiling of the chambers as living flagons of

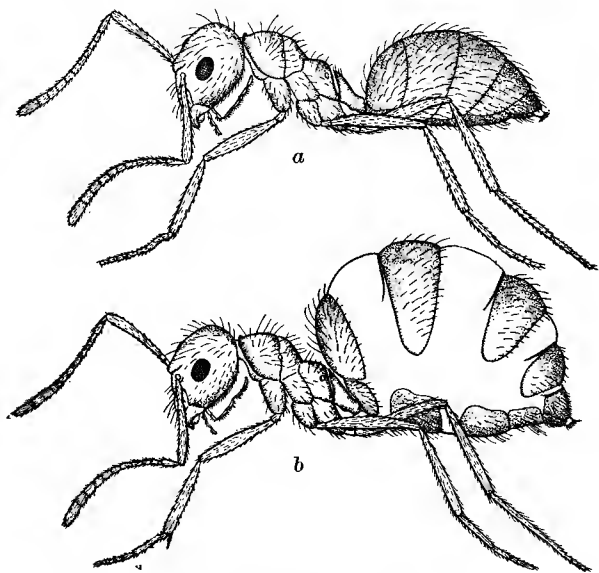


Fig. 26. *Prenolepis (Nylanderia) imparis* Say; a, worker in ordinary condition; b, replete.  $\times 12$ .

honey with animated necks and stoppers. Those who, in anthropomorphic mood, are wont to extoll the fervid industry and extraordinary muscular performances of ants should not overlook the patience and self sacrifice displayed by the replete *Myrmecocystus* as it hangs from the rafters of its nest, month in, month out, for years perhaps — a reservoir of temperamental as well as liquid sweetness.

We may now turn to a consideration of the honey ants described by various authors. The species may be arranged in two series, the first comprising certain forms that exhibit what may be called the semireplete condition — a stage somewhat in advance of incipient repletion, the second the forms that have attained the extreme of gastric distension. To the former belong the five first cases described below, to the latter only *Campo-*



*notus inflatus* and the *Myrmecocysti*. The transition from the semireplete to the perfect replete is represented by *Plagiolepis trimeni* and *Leptomyrmex rufipes*. In conclusion I have added a few remarks on a small group of Indomalayan *Cremastogaster* species, which have been regarded as honey ants.

### 1. *Prenolepis* (*Nylanderia*) *imparis* (Say).

This ant, which is the largest of the North American species of the genus, though it measures only 3–4 mm., is also the most widely distributed, ranging across the continent from the Atlantic to the Pacific in the transition zone. The typical form, which is dark brown or black, prefers to nest in clayey soil in shady places, but the smaller and paler variety *testacea* Emery occurs in pure sand. I have found both forms most abundant in the immediate vicinity of oak-trees, *testacea* in the pine barrens of New Jersey and the typical *imparis* in the rich woods of that state, Illinois and New York. The colonies rarely comprise more than 300 or 400 workers. The nests are never under stones, but always in the form of small craters, consisting of rather large, irregular earth or sand pellets, which at first sight resemble the pellets excavated by the smaller Attiine ants of the subgenus *Trachymyrmex*. *N. imparis* is a very timid, mild-mannered ant and lives very largely on the exudations of plants and the honey dew of aphids and coccids. The workers visit their pastures in files and return with their gasters greatly distended. Fig. 26 shows the difference between a depleted worker (*a*) leaving the nest and one returning with its gaster distended to its utmost capacity (*b*). In the latter the more heavily chitinized, brownish sclerites of the gaster are widely separated by the tense intersegmental membranes, through which shine, like an amber bead, the liquid contents of the crop. The gait of the depleted insect is very free and elegant, but when its crop is full it lumbers or waddles along in a very awkward fashion.

My attention was first called to the repletes of *Nylanderia* by my friend Prof. Harold Heath, who sent me a lot of specimens which he had been observing in California. With these he sent the following notes which I transcribe from his letter of April 15, 1901: "In our yard here in Palo Alto is a remarkably large nest of the *Prenolepis* among the roots of a live oak. This latter habitat is also shared by several colonies within a mile or so of the university, and there are numerous others living under the eucalyptus, cypress and other trees. In similar positions they occur widely through the Santa Clara Valley, especially about San José, where they also tunnel by the road sides and in bridle paths far up on the sides of the foot hills.

"Many of the colonies during the heat of the day remain comparatively

quiet, coming out during the morning and evening; but in several of the nests well-shaded, especially by the live-oaks, they are incessantly active throughout the day. In the nest here in the yard a continual incoming stream laden with food stuffs passes the procession going up the trunk and along the branches, and a careful search among the delicate twigs and leaves usually brings to light many individuals actively engaged in collecting food. This appears to be a waxy secretion which accumulates on the undersides of the leaves, on the stems and upon the buds of yet undeveloped leaves. It is certainly not the sap of the tree, for several twigs which I barked were passed over without notice. As many as ten individuals may occasionally be found at work on the underside of a single leaf, working their mandibles actively and gathering up small quantities of something which, as I have said, appears to be a waxy or resinous secretion. This is stored up by several individuals, possibly the majority, for the abdomens of those returning to the nest are as a usual thing somewhat larger than those of the members leaving it and appear more or less translucent. In perhaps one out of twenty the abdomen is twice the normal size, frequently giving such individuals a shaky, uncertain gait. The secretion has a sweet taste, sometimes also slightly acid, something like that of weakly acidulated honey.

"During the ascent of the tree several workers may stop as if resting and group themselves in a shaded fissure of the bark and remain for several minutes or even hours before proceeding on their journey, but so far as I have been able to observe, all of those *en route* for the nest never delay.

"Very frequently individuals are seen returning to the nest with withered oak-flowers or parts of insects. Their diet appears to be varied, as I have noticed in a colony kept in an artificial nest (Janet pattern), raw or cooked meat, insects and almost any substance with a sweetish taste being acceptable."

The late Rev. P. J. Schmitt, O. S. B., wrote me several years ago, that he had long been familiar with the replete habit of *Nylanderia*, and I have also had frequent occasion to see the ants visiting aphids and the extrafloral nectaries of *Ailanthus glandulosa* and other plants and returning to their nests with greatly distended gasters. The "waxy secretion" mentioned by Heath was probably honey dew or some substance analogous to that exuding from the galls of *Quercus undulata* in the Garden of the Gods. Kellogg (1905, p. 547, fig. 750) has recently mentioned the habits of *Nylanderia* and published a figure in which the distension of the gaster in the repletes is unduly exaggerated.

The replete habit is also observable in our North American species of *Prenolepis sensu stricto* (*P. parvula*, *bruesi*, *melanderi*) which are all much smaller insects than *Nylanderia* though of similar habit, except that they

very frequently nest under stones. In none of these species, however, are the repletes as numerous or as much distended as those of *imparis*. All of our species of *Prenolepis sensu lato* are peculiar in that the males and winged females which mature during late summer or early autumn, pass the winter in the maternal nests and celebrate their nuptial flight early in the following spring. It is probable that this hibernation of the virgin sexual forms is rendered possible, or at any rate facilitated, by the ability of the workers to store up liquid food, although in this respect they are very inferior to *Myrmecocystus*. This ability to store food may also account for the large size of the queens of *Prenolepis*, and especially of *Nylanderia*, as compared with the workers.

Our tiny *Brachymyrmex heeri depilis* Emery has habits very similar to those of certain *Prenolepis*. It lives a subterranean life under stones, cultivating root-coccids. The typical West Indian form of the species has been imported into Europe with tropical plants, and was first observed by Forel in the hot-houses of Switzerland. He says of this ant (1895): "I have observed specimens of *Brachymyrmex heeri* Forel with the gaster enormously distended with honey, but nevertheless running on the plants outside the nest; they had merely gorged themselves with the honey-dew of coccids and were returning home."

## 2. *Melophorus bagoti* Lubbock.

The Australian genus *Melophorus* is so closely related to *Myrmecocystus* that one of its species, *M. æneovirens* was long considered to belong to this genus. That *Melophorus* is also fond of living in arid regions is shown by the remarkable development of the ammochaetae or long circumoral bristles used in cleaning the fore legs and strigils. As I have shown in a former paper (1907a), all the series of these hairs (clypeal, mandibular, mental and gular) are present in *Melophorus*. In the New World *Myrmecocysti*, however, there are none on the mentum and in the Old World species there is a tuft on the mentum but none on the gula.

The genus *Melophorus* was based by Lubbock on *M. bagoti* in 1884. The types came from Central or Western Australia ("21° S. Lat."). Lubbock transposed the generic and specific diagnoses that had been written out for him by Forel, but the latter rectified the blunder a few years later (1886). *M. bagoti* is of a rich ferruginous red color and has polymorphic workers. The length of the smaller ones has not been recorded but that of the larger is 13-16 mm. In the latter the gaster is distended somewhat as in the *Nylanderia* repletes, and, as Forel has stated, is far from attaining the

amplitude of *Myrmecocystus*. The insect is undoubtedly able to walk about and in all probability does not hang from the roof of its galleries.

During the summer of 1907 Professor Forel kindly gave me a replete of *M. bagoti*, from which the accompanying figure was drawn (Fig. 27).

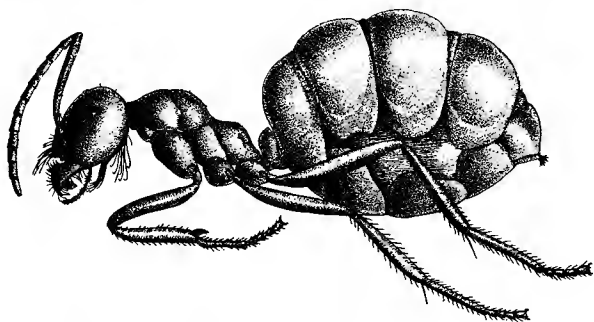


Fig. 27. *Melophorus bagoti* Lubbock, replete.  $\times 5$ .

In this specimen the gastric sclerites are greatly enlarged. Apparently they were originally much smaller but along their borders the intersegmental membranes seem to have hardened and turned brown secondarily. The lines representing the original lateral borders of the sclerites are shown in the figure.

### 3. *Melophorus cowlei* (Froggatt).

Froggatt (1896) described this ant as a *Camponotus*, but his figures and description show very clearly that it is a typical *Melophorus*, closely related to *bagoti*. Comparison of Froggatt's figures with Lubbock's and with the replete of *bagoti* in my collection, shows that the head in this species is broader than long and somewhat narrower in front than behind, whereas that of *cowlei* is distinctly longer than broad. This species also has a narrower thorax and the petiole of a different shape, judging from Froggatt's rather inadequate description. The replete, which measures 17 mm. has the gaster distended to much the same extent as that of *bagoti*, but the sclerites seem to be shorter and the intersegmental membranes larger.

Froggatt described all three phases of *M. cowlei* from specimens taken at Illamurta in the James Range and Spencer Gorge in the McDonnell Range, in the very center of Australia. He says that this ant is known to the natives as the "Ittootoonee" and gives the following notes sent him by Baldwin Spencer: "I came across a single nest of the golden yellow species, which was a small one, consisting of branching passages close to the sur-

face, under a little block of quartzite in one of the gorges amongst the McDonnell Ranges. In this nest the honey ants, though considerably swollen out, seemed to be able to move about slowly. Perhaps it was a young colony and they were not fully developed."

#### 4. *Leptomyrmex varians* Emery var. *rufipes* Emery.

This is the only honey ant known to occur among the Dolichoderinae. The genus *Leptomyrmex*, which is confined to Australia and New Guinea, is characterized by its very slender and emaciated body, extremely long legs and singular head. In 1882 Forel published the following note on *L. rufipes*: "In the excavated nests of this variety Mr. Turner found workers with the gaster considerably dilated by the crop full of transparent honey. The gaster resembled that of *Myrmecocystus*, without, however, attaining such dimensions." In an alcoholic specimen of this ant which I saw in Prof. Forel's collection, the gaster appeared to be much more distended than in the repletes of *Nylanderia* and *Melophorus*.

#### 5. *Plagiolepis trimeni* Forel.

This species was discovered by Mutschinson at Natal and described by Forel in 1895. The types were all repletes, 6.5 mm. in length, of which the head and thorax together measured only 2 mm. They are described as being of a "sordid brownish yellow color, more reddish on the head and thorax; the sides of the gastric segments brownish; feet and antennae yellowish." The gaster "is distended with honey, like a round cyst, transparent, as large as a hemp seed, on which the chitinous laminae of the segments appear as islands. The anterior portion of the first segment has a hollow depression in which fits the petiolar scale. With the aid of a lens it is possible to distinguish, below and behind, the stomach and gizzard with its reflected calyx, both of them displaced and flattened against the gastric wall." Forel further states that the gaster is "nearly as fully distended as that of *Myrmecocystus melliger*. . . . Locomotion must be almost impossible for this insect. Its appearance is that of a *Myrmecocystus* nurse *en miniature*." *P. trimeni* therefore represents a stage of repletion intermediate between *Nylanderia* and *Melophorus* on the one hand and *Myrmecocystus* on the other.

#### 6. *Camponotus inflatus* Lubbock.

Lubbock described the worker of this ant in 1880 from specimens taken

at Adelaide, Australia. His diagnosis was, however, so imperfect that the insect had to be redescribed by Forel (1886). McCook (1882) has also studied and figured this species (1882, Figs. 71 and 74). According to Forel, it "has nothing to distinguish it particularly from other *Camponoti*, except the purely physiological distension of its gaster, evidently due to the enormous plenitude of the crop, as in *Myrmecocystus melliger*. This dilatation, however, is smaller than that of *melliger*."

More recently (1896) Froggatt has described the male and female of *C. inflatus* from specimens collected at Ayers Rock, Illamurta in the James Range of Central Australia. All three phases of this ant are black with paler legs and antennæ. The repletes measure 17 mm. Froggatt records the following notes sent him by Baldwin Spencer: "The black honey ant (*Camponotus inflatus* Lub.) is called 'Yarumpa' by the natives, by whom it is esteemed a great luxury; it is, *par excellence*, the honey ant of the central country, and ranges across the Murchison in Western Australia. We found them plentiful in certain districts on the hard sandy plains, and also very abundant in patches among the Mulga scrub. The ground all round Ayers Rock, to the south of Lake Amadeus, was strewn with heaps of sand where the natives had been digging them out. They construct no mounds over their nests; the entrance, which is an inch in length by a quarter of an inch in width, leads down into a vertical shaft or burrow from five to six feet in depth. About a foot below the surface horizontal passages about a foot in length lead off from the main shaft, at the end of which were three or four of the honey ants, while the bottom of the main shaft, which is excavated into a larger cavity, contained a considerable number. The 'honey ants' are quite incapable of movement and must be fed by the workers. Unlike all the other ants noticed in this country, these did not appear to collect twigs, leaves or grass to carry into their burrows."

#### 7. *Cremastogaster inflata* F. Smith and *C. difformis* F. Smith.

As Frederick Smith's original account of these two Myrmicine ants (1857, 1858) has led to their being regarded as honey ants, we may properly include them in the present survey. Both species range from Tenasserim to Borneo through Burma, Java and Sumatra. *C. inflata* occurs also in the Philippines and *difformis* in Celebes. Of the latter species Emery has described a subspecies *physothorax* and a variety *mucronata*. In all these ants the gaster remains unmodified but the epinotum, or posterior portion of the thorax is greatly enlarged in *difformis* and even inflated in *inflata* (Fig. 28). In this species it is also of a honey-yellow color unlike the remainder of the body which is dark brown or black. Emery (1900) has also

described another species, *C. tumidula* from Sumatra, which shows an incipient stage in the expansion of the epinotum.

Smith stopped long enough in the series of his often hopelessly inadequate specific diagnoses to pen the following remarks on *C. inflata*: "This is one of those singular and anomalous species, which, without any particle of information, derived from observation, puzzle and perplex the naturalist; what can possibly be the use of the bladder-like excrescence on the thorax of this insect, it is difficult to imagine; to the touch it is elastic, and apparently forms a receptacle for saccharine fluids. With the aid of a microscope, a small circular orifice can be seen at each of the posterior lateral angles of the swollen part, and small crystallized particles are apparent, not only within the orifice, but scattered over the surface of the inflation; we may, therefore, reasonably suppose that this singular apparatus is for the purpose of elaborating a suitable and necessary aliment for the larvæ of this singular insect." Of *C. difformis* he says: "This species resembles the *C. inflata* in form; but the swollen portion of the thorax is of a solid consistency; it forms, however, a similar laboratory of saccharine matter; the orifice from which it exudes is not exactly at the posterior angles, but a little way beneath; in some specimens, masses of crystallized particles can be seen beneath the orifice of this species, both large and small workers have been examined, and the same apparatus is found on them both."

More recently Bingham (1903) has made a few observations on these ants which he describes as follows: "*C. difformis*, *physothorax* and *inflata* have the metathorax remarkably large and swollen, with a hollow in each side interiorly, communicating exteriorly by a tiny aperture. In live specimens there seems to be a continual flow from this aperture of a sweet fluid, and I have watched the workers of *C. physothorax* licking one another's thoraces vigorously."

These brief but interesting notes do, indeed, leave the reader in some perplexity. Janet (1898) surmised that the epinotal enlargement in *C. inflata*

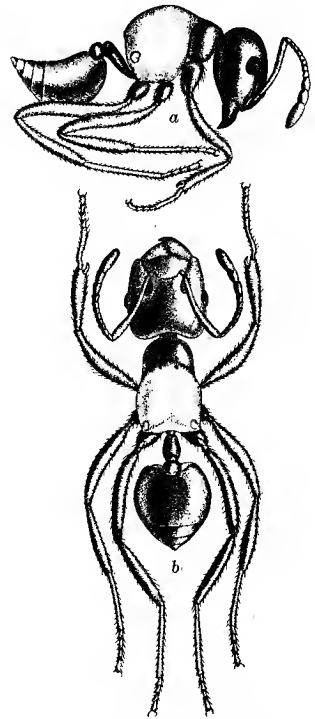


Fig. 28. *Cremastogaster inflata* F. Smith, worker; a, lateral, b, dorsal view.  $\times 8$ .

might be due to hypertrophy of the peculiar glands which he, Meinert and Lubbock had found in this portion of the thorax of our northern ants. These structures, which Janet studied and figured with great care, consist of a pair of chambers each opening to the exterior by means of a button-hole-shaped orifice on the metasternum. The glands proper open into these chambers, which contain hair-like organs apparently for the diffusion of the secretion. In a number of specimens of *C. inflata* in my collection, from Zamboangan, Philippines, two broadly elliptical or nearly circular openings are seen on each side of the epinotum (see Fig. 28a). The upper, which is somewhat smaller, is the tracheal orifice, or stigma, the lower is undoubtedly the external opening which leads directly into one of the large inflated cavities. As all of my specimens are dry and carded, I am unable to ascertain the histological structure of these organs. I am convinced, however, that they represent, as Janet supposed, an enormous development of the organs found in the corresponding portion of the epinotum of our common ants. This is also indicated by an examination of specimens of *C. difformis* from Perak and of *mucronata* from Sumatra. In these the openings of the epinotal chambers are more ventral and more slit-shaped than in *inflata*, and may therefore be described as intermediate between those of *inflata* and our northern species of *Cremastogaster*.

As the function of the metasternal glands even in our common ants is still unknown, we can hardly expect to form a satisfactory conception of the hypertrophied homologues of these organs in a few Indomalayan species that have hardly been studied in a living condition. That these organs should secrete a sweet liquid to be fed to the ants or to their young is surprising at first thought and suggests the nursing habits of the Mammalia, but when we stop to consider that ants are in the habit of feeding their young and one another with a secretion of the labial, or salivary glands, we can see no reason why, in certain species, thoracic glands might not be developed for a similar purpose. It will be very interesting, nevertheless, if future investigation proves that certain species of *Cremastogaster*, a genus whose members are so conspicuously fond of feeding on the saccharine excrement of aphids and coccids, have themselves developed a capacity for distilling a substance resembling honey dew. It should be possible, since *C. inflata* occurs in the Philippines, for some of our entomologists, who have an opportunity to visit these islands, to investigate this interesting subject which was first suggested by Frederick Smith half a century ago.



## CONCLUSION.

In the foregoing pages the habit of developing repletes has been shown to recur sporadically in some six different genera of ants, namely, *Prenolepis*, *Melophorus*, *Plagiolepis*, *Leptomyrmex*, *Camponotus* and *Myrmecocystus*. We are therefore dealing with a case of convergent development and as in other cases of this kind, we are led to determine the external conditions that must act as the common stimulus in calling forth this peculiar adaptation on the part of such different ants. The geographical distribution of the various honey ants points to drought as one of the most important of these conditions, for nearly all of these insects are confined to the dry plains and deserts of North America, South Africa and Australia. Forel seems to be the only author who has noticed this peculiarity in the distribution of these insects. He says (1902): "The extraordinary distension of the crop seems to be frequent in the Australian species of the genera *Melophorus*, *Camponotus* and *Leptomyrmex*. I suppose that this is due to the extremely dry climate of the country, which must compel the ants to remain, often for long periods, in their subterranean abodes. At such times a store of provisions in living bags must be very useful to them."

There can be little doubt of the truth of this statement, but I believe that it should be expressed in a different manner. The impulse to develop repletes is probably the brief and temporary abundance of liquid food (honey dew, gall secretions, etc.) in arid regions and the long periods during which not only these substances but also insect food are unobtainable. The honey is stored in the living reservoirs for the purpose of tiding over such periods of scarcity, and the ants remain in their nests because they do not need to forage. Hence the confinement mentioned by Forel is not the immediate but one of the ulterior effects of drought, for I am convinced from my observations on desert ants that no amount of dryness will keep these insects in their nest when they are in need of food.

*Nylanderia imparis* would seem to be an exception to the general rule of distribution in the honey ants, since the typical form of this species occurs in rather shady places and in clayey soil which holds moisture rather tenaciously. It is not improbable, however, that what is known as var. *testacea* Emery is really the ancestral form of this species. This ant nests in sandy soil and is one of the most abundant insects in the pine barrens of New Jersey and in similar localities in the Eastern States. Now these are xerophytic regions, as shown by the pines, scrub oaks and many other plants, and the sand in which this vegetation grows does not retain water readily and therefore presents conditions not unlike those of the deserts and great plains.

The dark colored typical *imparis* is much less abundant and probably represents a secondary adaptation to moist woods and firmer soil. This would account for the persistence of repletes in an ant inhabiting rather humid, shady localities.

Most ants of temperate, mesophytic regions have a mixed diet, consisting of insects, honey dew and plant excretions. When such species come to live in deserts or other arid regions, where the long droughts of summer and the cold of winter restrict plant and insect life to a brief season, they usually take on one of the four following adaptations:

1. They may exaggerate the insectivorous habits which they already possess, and become intrepid, ravenous, hunters. They thus manage to secure a sufficient amount of food even under unfavorable conditions. This adaptation is beautifully shown in the Old World *Myrmecocysti* which are represented by the greatest number of species, subspecies and varieties in the deserts of North Africa. The same tendency, however, is apparent in the American races *orbiceps* and *mendax*.

2. Many species have taken to eating and harvesting seeds — a very obvious adaptation to arid regions covered with a short-lived herbaceous flora, as is shown by the species of *Pogonomyrmex* in the New World, *Messor*, *Solenopsis* and *Pheidole* in both hemispheres, and *Holcomyrmex*, *Oxyopomyrmex*, *Goniomma*, *Meranoplus* and *Pheidologeton* in the Old World. These ants still feed upon insects when these are obtainable, but seeds furnish such an inexhaustible and nutritious food supply that the habit of collecting and storing them in the nests has become highly developed.

3. A number of species, the honey ants, which have been described in the foregoing pages, have taken to storing the sweet exudations of plants and the excretions of aphids and coccids in the crops of a physiological caste, the repletes.

4. Some ants manage to live and thrive in arid regions because they cultivate and eat fungi. This habit, which I have described in detail in a recent article (1907b), is peculiar to a single tribe of American Myrmicine ants, the Attii, and probably originated in the luxuriant rain-forests of the tropics. Thence several of the species have migrated into the deserts of Northern Mexico and the southwestern states, where they can always obtain the vegetable débris for the substratum on which to grow their fungi and where these delicate plants can be successfully cultivated some distance below the dry surface of the soil.

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